ECOLOGICAL EFFECTS OF SPAWNING SALMON ON SEVERAL SOUTHCENTRAL ALASKAN STREAMS

A

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Abstract

The ecological effects of salmon (*Oncorhynchus* spp.) carcasses on southcentral Alaskan streams were studied by: (1) observing salmon carcass decomposition and use; (2) comparing the macroinvertebrate community structure of streams receiving different inputs of salmon carcasses; and (3) quantifying the amount of marine-derived nitrogen (MDN) entering stream food webs using stable-isotope analysis. Abiotic mechanisms, such as large woody debris and the slow waters of stream margins and eddies were important in initial retention of salmon carcasses. Once entrained, carcasses decayed rapidly due to intense microbial processing. Stream insects and fishes were observed consuming carcasses, eggs, and smolts. Macroinvertebrate communities in streams receiving runs of salmon or in lake outlet streams were more diverse taxonomically. One functional feeding group, filterers (including net-spinning caddisflies (Hydropsychidae) uncommon in Alaska), increased in relative abundance. Although many other taxa also responded positively to enrichment, some taxa responded negatively. A significant difference existed in $\partial^{15}N$ values between MDN and terrestrial sources but natural dissolved inorganic nitrogen contributions to stream food webs (≈90-95% of total N) from groundwater generally overwhelmed the marine signal (≈5-10% of total N). $\partial^{15}N$ values generally suggested that some MDN (≈15% of total N) entered into food webs after its incorporation into algal biomass but values for certain macroinvertebrate taxa (*Arctopsyche* and *Plumiperla*), salmon fry (*Oncorhynchus* spp.) grayling (*Thymallus arcticus*), rainbow trout (*O. mykiss*) and American dippers (*Cinclus mexicanus*) suggest these biota directly consume substantial amounts (40%-90%) of salmon protein. $\partial^{15}N$ values in individual macroinvertebrate taxa usually cycled seasonally. All three elements of this investigation support the hypothesis that salmon carcasses can be important in structuring aquatic food webs.

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Chapter 1-Overview

Migratory fishes and waterfowl constitute a potentially large seasonal subsidy of energy and nutrients to lakes, streams, and wetlands (Parmenter and Lammara 1991). For small streams, plant detritus generally constitutes the major food source for consumer food webs (Minshall 1978, Vannote et al. 1980). Plant detritus is of relatively low food quality compared to animal material. Animal carcasses are likely to be an especially important contribution of nitrogen (C/N ratio <7) compared to leaf litter from riparian trees (C/N ratio≈20-80) (Cummins and Klug 1979). Fish carcasses are highly concentrated sources of phosphorus: in Mirror Lake, New Hampshire, O'Brien (1985) estimated that the phosphorus content of a 1 kg fish (≈2g phosphate) would exceed the phosphate content of 100 m^3 of lake water (≈ 1.6 g). Animal carcasses thus represent highly concentrated packages of nutrients. Carcasses contribute in two important ways to freshwater ecosystems: by decompositional release of inorganic nutrients and by direct consumption of carcasses by consumer organisms.

The potential role of salmon (*Oncorhynchus* spp.) carcasses in linking the marine environment and fresh-water systems has long been recognized (Juday et al. 1932, Donaldson 1967, Brickell and Goering 1970, Krokhin 1975, Richey et al. 1975, Schell and Zieman 1989). In Alaska, scientists have intensively investigated the biological enrichment of sockeye salmon (*O. nerka*) systems (Kline et al 1986,1989; Mathisen 1972; Mathisen et al. 1988). Also in Alaska, Koenings and colleagues (Koenings et al. 1986; Koenings and Burkett 1987; Kyle et al. 1988) have investigated the relationships between system fertility and production of sockeye salmon.

Sockeye salmon systems differ fundamentally from systems receiving runs of other salmon species. Sockeye salmon spawning and carcasses contribute nutrients to lake ecosystems: these nutrients fertilize lake planktonic food chains supporting zooplanktivorus sockeye fry. In contrast, other species of salmon spawn in riverine systems, contributing nutrients and carbon to benthic 'biofilm' (algae and heterotrophic microbes) and to food chains based on scavenging consumers. This study concerns the roles of salmon carcasses in stream food webs; thus review of past research is largely confined to the literature of running waters.

Minshall et al. (1991) examined algal biomass on tiles upstream and downstream of rainbow trout carcasses placed in an Idaho stream. There was no evidence of enhanced algal growth downstream of carcasses and the authors suggest that nutrients from carcasses were used by decay microbes on the carcasses. In contrast, Richey et al. (1975) found that periphyton biomass and production, activity of heterotrophic microbes, and nutrient concentrations were greater downstream of the spawning area of kokanee salmon (*O. nerka*) in a California stream. Likewise, Sugai and Burrell (1984) suggested that decomposition of spawned salmon accounted for seasonal peaks of phosphorus and nitrogen in a mixed pink and chum salmon spawning stream in southeast Alaska. Spawning migrations of the anadromous alewife (*Alosa pseudoharengus*) (approximately 39-57% mortality during spawning) in U.S.A. Atlantic Coast streams had profound ecosystem effects (Durbin et al. 1979). Nutrient (nitrogen/phosphorus) and carbon inputs from spawner mortality and excretion were much greater than nutrient losses from out-migrations of young. Nutrients and carbon inputs

enhanced decomposition rates of leaf litter and increased primary production.

There is a well-developed literature on carcass decomposition in terrestrial systems (e.g., see Payne 1965), primarily from a forensic perspective (e.g., use of carrion insect fauna to estimate time of death). In contrast, the natural history of carcass use and decomposition in freshwater systems has received little attention. Carcasses are used by a great diversity of aquatic and terrestrial organisms, ranging from bears (*Ursus* spp.) to decay microbes. Cederholm et al. (1985, 1989) experimentally released salmon carcasses into spawning streams on the Olympic National Park, Washington. Carcasses showed little downstream movement: most were retained in the stream or riparian zone, with few carcasses flushed beyond 600 m despite high-flow events. The percentage of fish mass eaten by mammals (14 species) and birds (8 species) ranged from 30-79%, although historical salmon runs were much greater (possibly saturating demands of mammals and birds).

The role of invertebrates in carrion decomposition is unclear. Parmenter and Lamarra (1991) followed decomposition of fish and waterfowl carcasses in a Wyoming freshwater wetland and noted use of floating carcasses by flesh flies (Diptera: Sarcophagidae) and blow flies (Diptera: Calliphoridae) but no use of floating carcasses by aquatic invertebrates. Minshall et al. (1991) placed rainbow trout carcasses in an Idaho stream (inhabited only by nonanadromous fish) and suggested that although stream macroinvertebrates were abundant on carcasses, the invertebrates appeared to play little role in decomposition. In contrast, Brusven and Scoggan (1969) observed caddisfly larvae actively feeding on squawfish carcasses. Even if stream macroinvertebrates are responsible for consuming only a small proportion of fish carrion, they may play an important role in opening up the

skin and carcass to microbial invasion. It is unknown what, if any, functional groups (Cummins and Klug 1979) of aquatic invertebrates will eat salmon carcasses in Alaskan streams and whether or not a clear succession of invertebrate communities will exist as found with terrestrial carcasses (Payne 1965).

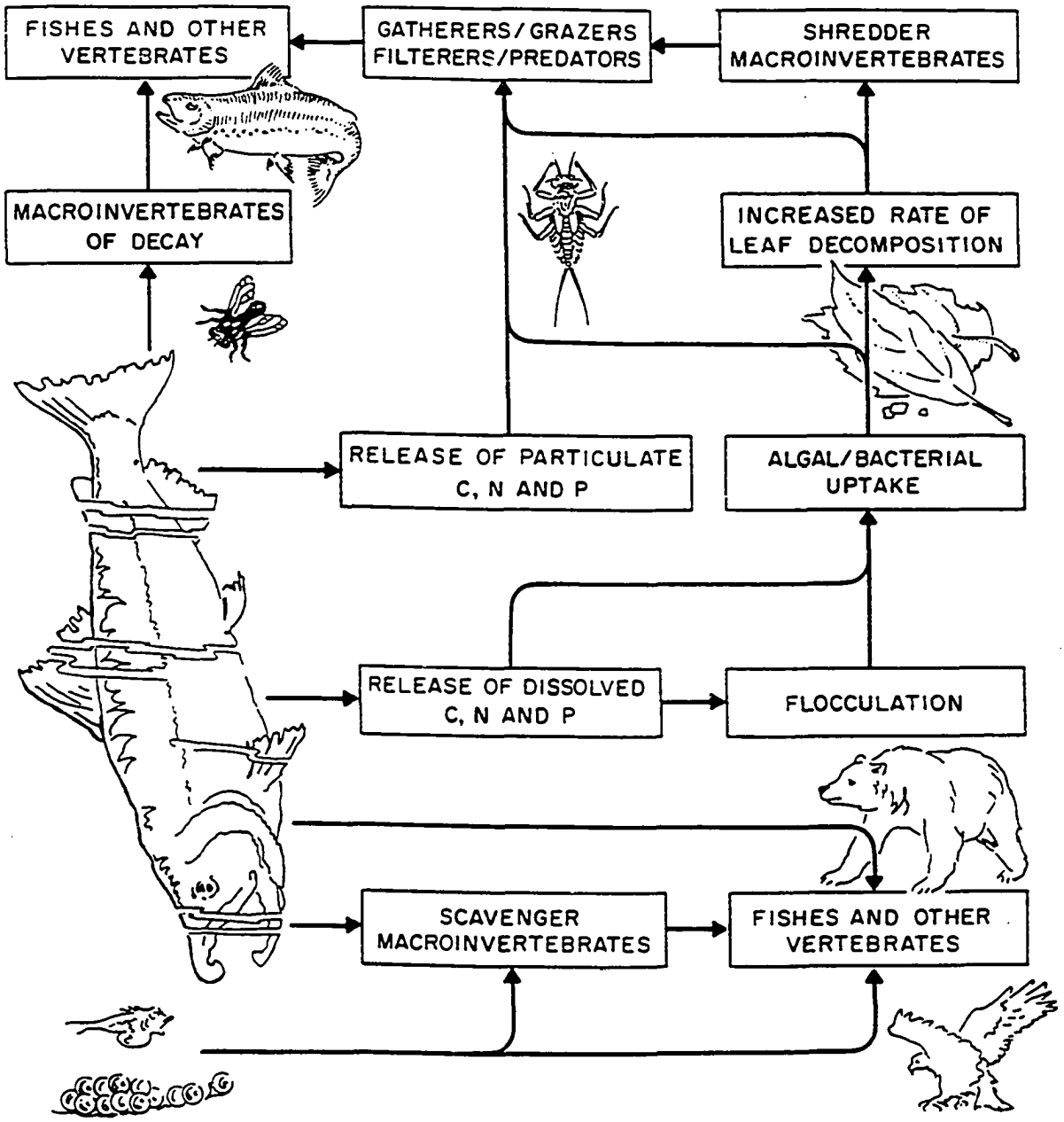
Perhaps more importantly, Anderson (1976) and Anderson and Cummins (1979) suggested that ingestion of animal material (especially late in the larval or nymphal growth cycle) may be critical to growth of many stream invertebrates, including detritivores and herbivores. Thus, findings of large number of many taxa of stream invertebrates on fish carrion may indicate that carcasses supply a critical subsidy of high quality animal protein.

It is very difficult to obtain direct information on scavenger diets via observation. Even relatively easily observed large vertebrates (e.g., mammals and birds) are often elusive or nocturnal. Obviously, tracing transfers of dissolved organic carbon and plant nutrients leaching from carcasses by observation is impossible. Examination of gut contents only provides information on ingestion of foods (not assimilation) and is limited to recent foods. Fortunately, stable-isotope techniques allow tracking of different food sources through food webs, so long as the food sources have a sufficiently distinct stable-isotope signature. The ratio of stable-isotopes in consumer tissues reflects long-term assimilation of food sources (Rounick and Winterbourn 1986). The use of stable-isotopes to trace food webs has been reviewed in Peterson and Fry (1987), Rounick and Winterbourn (1986), Rundel et al. (1989), and Coleman and Fry (1991). Stream ecologists in New Zealand have made extensive use of carbon stable-isotopes to trace stream food webs (Winterbourn et al. (1984); Rounick and Hicks 1985; Winterbourn

et al. (1986); Collier and Lyon 1991). In Alaska, Schell and Zieman (1989) used a combination of stable and radioactive isotopes of carbon to trace the contribution of 'old' carbon derived from peat to freshwater and marine food webs on the North Slope. Kline et al. (1989) used stable-isotopes of carbon and nitrogen to distinguish contributions of marine-derived nutrients to Sashin Creek, SE Alaska. This investigation demonstrated that marine-derived nitrogen from salmon spawning constituted the dominant source of nitrogen for food webs in the spawning area.

Simply summarized, carcasses potentially contribute flesh directly to both terrestrial and aquatic scavengers and supply dissolved nutrients and carbon to stream food webs (Figure 1.1). The purpose of this study was to investigate the effects of inputs from salmon carcasses on several non-coastal Alaskan spawning streams. The first goal was to describe the natural history of salmon carcass decomposition in lotic systems, describing use of carcasses by the stream biota, most importantly macroinvertebrates. The second goal was to compare the taxonomic composition of benthic macroinvertebrate communities in salmon-enriched and salmon-excluded streams before, during, and after salmon runs. This would establish whether and how seasonal inputs of marine-derived nutrients and energy affect macroinvertebrate community structure over time. The third goal, again using salmon-excluded streams as controls, was to employ stable-isotope techniques to map the fate of marine-derived nitrogen and carbon from salmon through stream and riparian food webs.

Figure 1.1 Diagram of potential effects of salmon carcasses on spawning streams.



Chapter 2----Natural history of salmon decomposition in southcentral Alaskan streams

INTRODUCTION

Whereas anadromous salmon obviously deliver nutrients and energy directly to terrestrial and aquatic consumers (e.g., bears eating salmon and resident fishes consuming salmon eggs), the extent to which affected ecological communities along upper reaches of streams depend upon the yearly flush of marine-derived foodstuffs for support is undetermined. Despite the strongly oligotrophic nature of watersheds in Alaska, systems having salmon runs appear to display high production of aquatic invertebrates, fish, birds and mammals. Live and dead salmon are undoubtedly significant, if not essential, components of many northern food webs.

Overall, the natural history of salmon carcass decomposition has received limited attention. Bald eagles (*Haliaeetus leucocephalus*), various waterfowl, and grizzly bears (*Ursus arctos*) all depended on the historically large kokanee (land-locked red salmon (*Oncorhynchus nerka*)) spawning run in tributaries of Flathead Lake (Spencer et al. 1991). High retention rates of salmon carcasses occur on the Olympic Peninsula, Washington where 22 species of birds and mammals consume them (Cederholm et al. 1989). Bears living near the Karluk River, Kodiak Island, Alaska, prey on adult salmon but switch to berries for food when salmon numbers are low (McIntyre et al. 1988). Resident brown trout (*Salmo trutta*) in tributaries of Lake Ontario seasonally rely on salmon eggs as their major source of food (Johnson and Ringler 1979a).

Only a few studies address direct insect use of fish carcasses. Trichoptera

larvae were noted eating dead squawfish (Brusven and Scoggan 1969) and blowfly larvae (Diptera: Calliphoridae), apparently feeding on salmon carcasses in a stream, were eaten by young salmon and trout (Johnson and Ringler 1979b). In a laboratory experiment, stonefly nymphs (Plecoptera) ate steelhead (*O. mykiss*) eggs and alevins (Claire and Phillips 1968). Scavenging of carcasses by both aquatic and terrestrial macroinvertebrates has been observed by myself and others (Kline et al. 1989).

Although Minshall et al. (1991) noted no increase in algal biomass downstream from rainbow trout (*O. mykiss*) carcasses, apparently due to tight nutrient spiraling, Richey et al. (1975) found that periphyton production, heterotrophic microbe activity, and nutrient concentration were greater downstream of a spawning area of kokanee in a California stream. Durbin et al. (1979) reported increased nutrients from spawning alewives resulted in greater primary production, heterotrophic production, and enhanced decomposition of leaf detritus. Surprisingly, no literature was found reporting either bacterial or fungal taxa or their dynamics on salmon carcasses.

The purpose of this study was to investigate the natural history events of salmon carcass decomposition in southcentral Alaska streams. This includes describing deterioration of carcasses, reporting their use by watershed biota and determining rates of carcass decomposition. This information will give a broader perspective on marine-terrestrial linkages, assisting both aquatic and terrestrial resource managers.

I hypothesize differential use of salmon carcasses by the various functional groups of aquatic macroinvertebrates will result in different

community structures depending upon degree of salmon enrichment.

MATERIAL AND METHODS

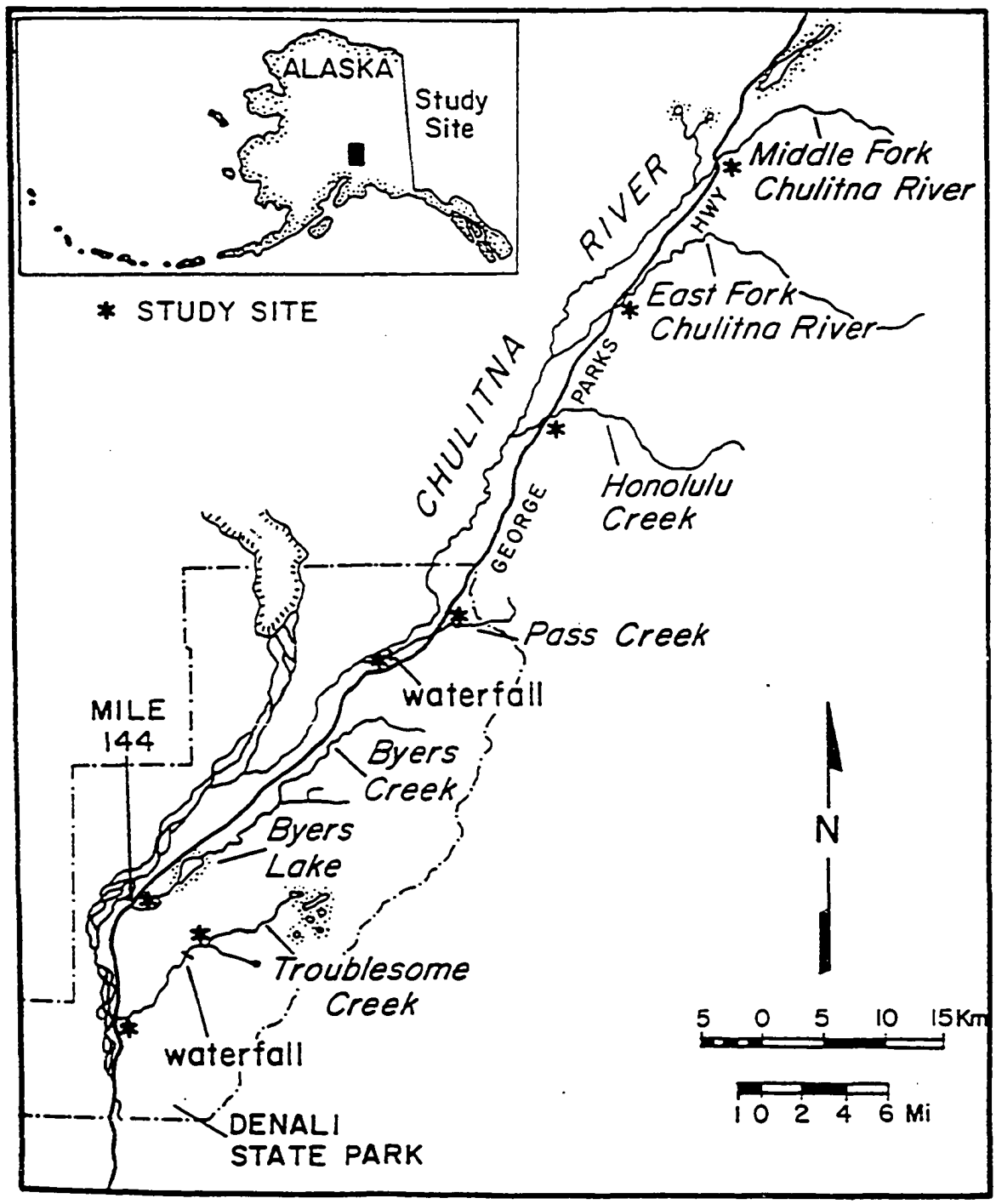
Study sites

The principal study streams are located approximately 140 km NNE of Anchorage in southcentral Alaska near 63°N 00′ N 149° 30′ W (Figure 2.1). Located south of the Alaska Range, they drain the Talkeetna Mountains and flow into the Chulitna River. The Chulitna River in turn, flows into the Susitna River, which flows to Cook Inlet and the North Pacific Ocean. The study sites, readily accessible by the Parks Highway, are located on six 3rd and 4th order (Strahler 1969) streams (based on U.S. Geological Survey maps, 1:63,360 scale). Discharge was determined using a Pygmy meter, using protocol described by Hewlett (1982), once monthly for July, August and September in 1993. Discharge varied from 1.5 $m^3 \cdot sec^{-1}$ to 20 $m^3 \cdot sec^{-1}$ depending upon the site and recent precipitation. The study streams were Troublesome Creek, Byers Creek, Pass Creek, Honolulu Creek, East Fork of the Chulitna River and Middle Fork of the Chulitna River.

Byers Creek has runs of all five species of Pacific salmon: king/chinook (*O. tshawytscyha*), red/sockeye (*O. nerka*), silver/coho (*O. kisutch*), dog/chum (*O. keta*) and pink/humpy (*O. gorbuscha*). Compared to Byers Creek, both Lower Troublesome and Lower Pass Creeks have similar runs of king, smaller run of silvers, dog and pink salmon but no runs of red salmon. The Middle Fork of the Chulitna River, the East Fork of the Chulitna River and Honolulu Creek all receive sparse runs of king salmon (unpublished).

On one occasion, salmon carcasses were examined from drainages located in interior Alaska. These watercourses were the Kaltag River (≈490 km west of Fairbanks near 64° 30′ N 158° 00′ W) and the Clearwater River

Figure 2.1 Map delineating study stream location. Inset locates study area in Alaska. Asterisks mark study sites.



(≈140 km east of Fairbanks near 64° 50′ N 149° 20′ W). Estimated flows were 10 $m^3 \cdot sec^{-1}$ and 15 $m^3 \cdot sec^{-1}$ respectively. Both rivers eventually flow into the Yukon River, which flows into the Bering Sea. The Kaltag River has runs of king, dog, and silver salmon while the Clearwater River has only dog and silver salmon. The latter is spring fed while the former in not. Both are 4th order streams.

Decomposition rates of salmon carcass were investigated at Clear Creek (≈100 km southwest of Fairbanks near 64° 10′ N 145° 30′ W). This is a spring-fed stream (est. flow ≈3 $m^3 \cdot sec^{-1}$ though only 2nd order) that eventually drains into the Yukon River thence to the Bering Sea. From August through October Clear Creek has runs of dog salmon and silver salmon.

General natural-history information

During the late summers of 1988-1993, surveys of study streams were made. During these trips, salmon carcasses encountered in streams were examined for macroinvertebrates. I wore shoulder-length rubber gloves to remove carcasses from the stream before counting macroinvertebrates present on the carcass. Numbers recorded are conservative because variable numbers of invertebrates were dislodged during removal of the carcasses from the benthos. Observed losses were often as high as 75+% of macroinvertebrates originally present. Also, counts were undertaken without ocular aids so early instars undoubtedly were missed in thick fungal mats often present on salmon carcasses. The salmon carcasses collected from the Clearwater River during November 1990 were not examined individually. On this stream, Commercial Fisheries Division personnel of the Alaska Department of Fish and Game removed 10 carcasses from the benthos and

placed them in an 80 l plastic tub. Most macroinvertebrates still clinging to the carcasses then crawled off, falling into the holding tub. These, and the few remaining invertebrates on the carcasses, were identified. The average number per carcass was estimated by dividing the total number of macroinvertebrates found by the number of fish in the tub.

Rainbow trout, longnose suckers (*Catastomus catastomus*) and grayling (*Thymallus arcticus*) were collected with sport-fishing gear providing stomachs for casual field analysis of recently ingested food items. Dippers (*Cinclus mexicanus*) collected with a shotgun provided similar information. Anecdotal observations involving salmon carcass use by macroinvertebrates, fish, birds and mammals gathered while on collecting trips were recorded.

The general pattern of physical disintegration of salmon carcasses, from post spawned but alive fishes, to the final scattered bones and particles of flesh, was recorded.

Salmon carcass deterioration rates

During late July 1993, dog salmon in pre-spawning condition were caught in a gill net (2 by 20 m with 11 cm stretched mesh) placed in the Tanana River 10 km west of Fairbanks, Alaska. These fish were immediately frozen. They ranged in weight from 1.9 kg to 3.5 kg. On 1 September 1993, ten were placed in Clear Creek, a spring-fed spawning stream near Anderson, Alaska approximately 100 km southwest of Fairbanks, Alaska. The carcasses were placed in a run of the creek (approximately 0.5 m deep and 10 m wide) located five km north of the town of Anderson and 300 m downstream from the salmon weir operated by the Alaska Department of Fish and Game on that creek.

Salmon carcasses were measured to the nearest centimeter from the tip of their nose to the fork in their tail, weighed to the nearest 50 gm with a 0 to 5 kg spring scale (Ohaus Corporation, Florheim Park, New Jersey), and sexed using external morphology. A wire was fastened through their gills and around their heads, and individually tied to 0.5 m pieces of 1.27 cm rebar that had been pounded into the streambed enough to secure the salmon in a location on the benthos free from substantial turbulence. On 1 October 1993, three of these fish were removed, placed in a plastic bag and frozen. They were replaced with five frozen fish. This cycle was repeated 1 November with the seven remaining original fish removed, three of the October placement fish removed while four frozen fish were placed in the run. On 1 December, the remaining two October-placed fish were removed along with two fish from the November placement. On 1 January, 1994 the remains of the last two fish from the November placement were removed from the creek, placed in plastic bags, and frozen.

Because water content of carcasses is highly variable, original dry weights of carcasses were estimated by determining dry weight:wet weight ratios of three male and two female fresh salmon (the proportion of low water content gonadal tissues differs between sexes). Following determination of wet weight, each was chopped into small chunks (<5 cm^2) to increase surface area for fast drying. The samples were then placed in pre-weighed enamel-coated metal trays, dried at 50°C for 1 week, after which no further weight loss was noted. The dessicated remains were weighed and original percent dry weight:wet weight ratio determined. All decomposing salmon collected during this study were dried and weighed as noted previously.

Percent loss in dry weight from estimated original dry weight was interpreted as percent decomposition over time.

RESULTS

Deterioration of salmon carcasses in streams

The initial agent of salmon decomposition was the salmon itself. During spawning activities, most fish severely abrade themselves while building redds and defending territories. Spawned-out, but still alive, fish often have exposed flesh on the head, tail and ventral regions. These abrasions surely facilitate entry of microbes. Because the salmons' immune system is functioning poorly during spawning, intense systemic microbial infections follow through these abrasions (Groot and Margolis 1991). Many dying or recently dead fish have carpet-like patches of fungus of various extent on their bodies (Figure 2.2). Several incompletely spawned pink salmon, still vigorously alive but blinded by fungus, which covered their eyes, were noted in Byers Creek during August of 1988.

The common behaviour of post- spawned fish is to seek slow and shallow waters, which no doubt aids in initial stream retention of carcasses after their death. Carcasses are also commonly detained by large organic debris, entrained onto the stream bed in eddies behind medium and large boulders or stopped by riffles (Figures 2.3, 2.4, and 2.5). One spruce tree stump and root mass (≈1.75 m diameter) in Byers Creek held 37 pink salmon in August 1988. Stream and terrestrial invertebrates and vertebrates commonly were observed feeding on abraded muscle tissue on carcasses during the initial entrainment period. The former includes numerous taxa of aquatic invertebrates (Table 2.1) and terrestrial blowflies. Resident and rearing

Figure 2.2. Recently dead salmon displaying abundant fungal growth at base of both pectoral fins, the ventral region below gills and on its side.

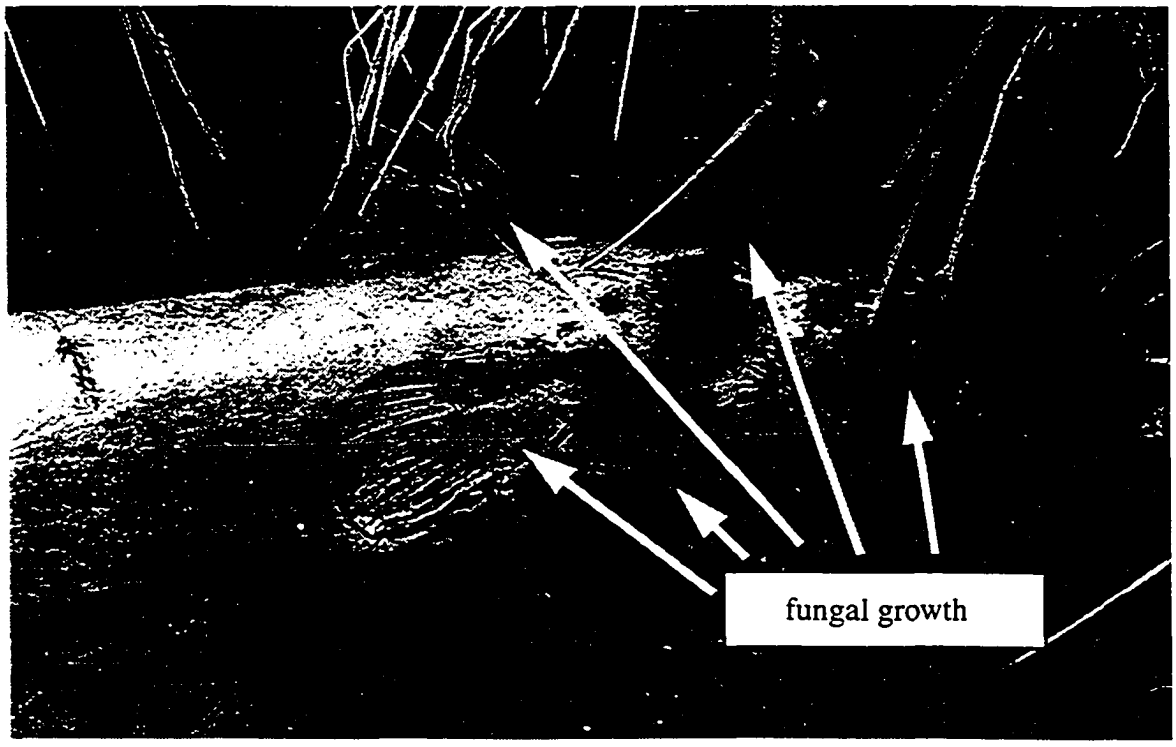


Figure 2.3. Large (15+ kg), dead king salmon entrained on small rock and brush in stream.

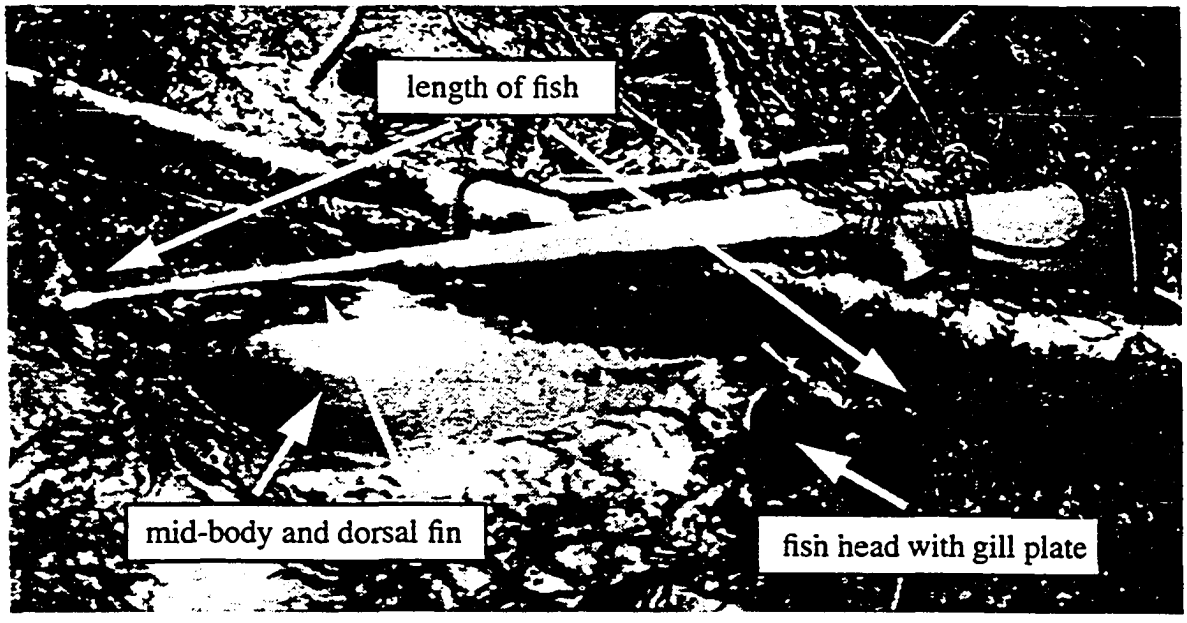


Figure 2.4. King salmon stranded by falling water levels on dry stream bed

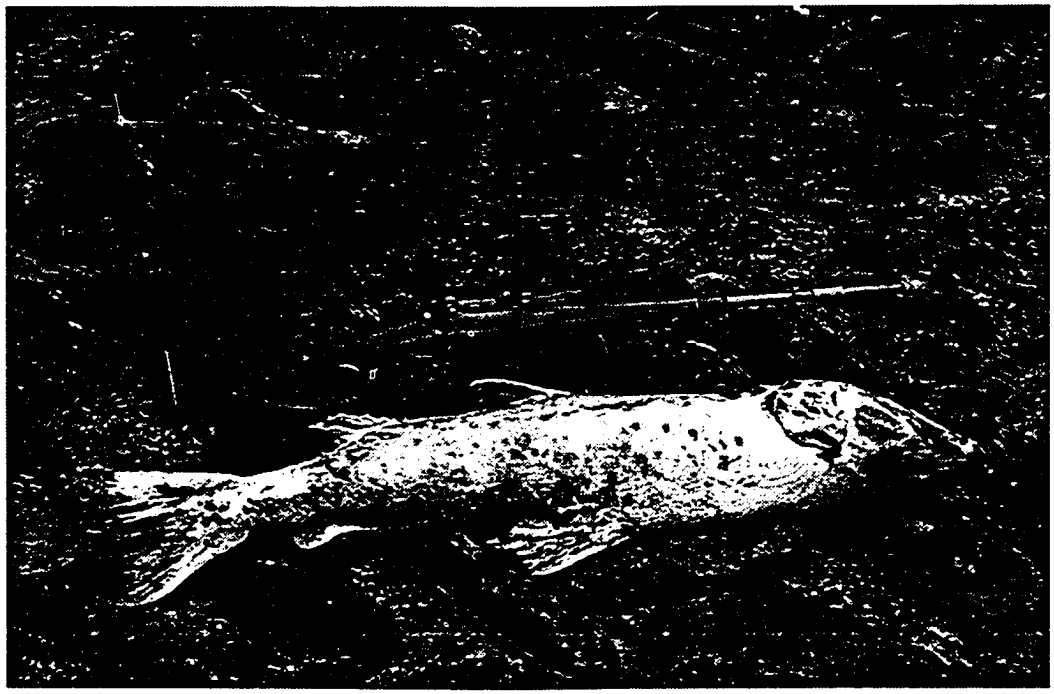


Figure 2.5. Pink salmon, much smaller than kings, are often windrowed in shallow waters or against stream structure.

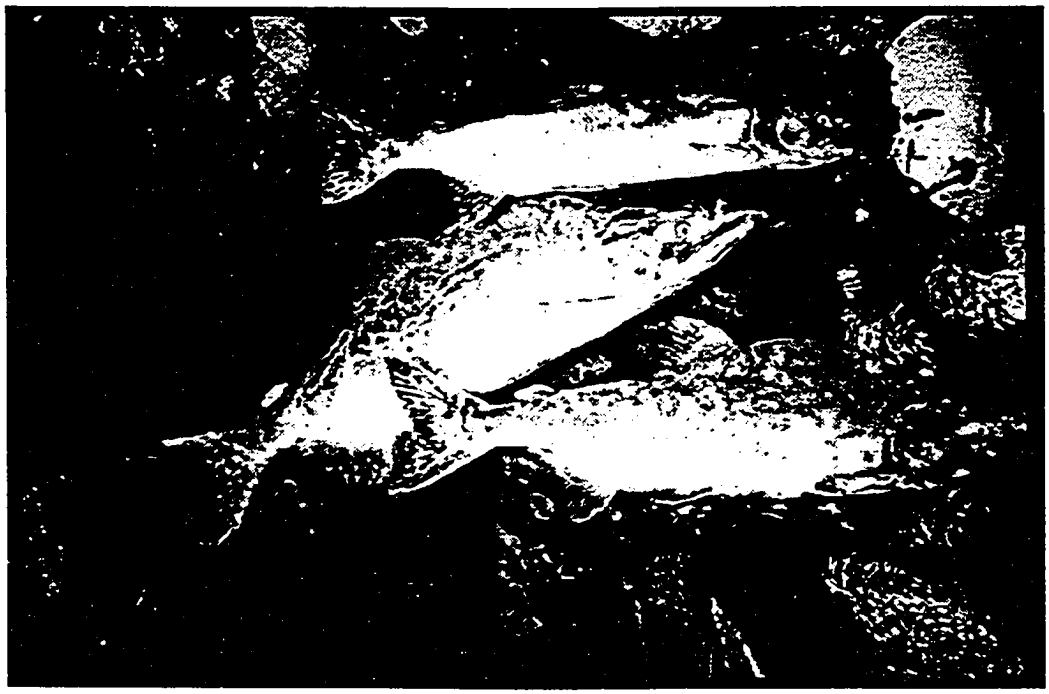


TABLE 2.1. Lotic macroinvertebrate taxa observed on 31 salmon carcasses in southcentral and interior Alaska streams. The notation '(n)=#' refers to the number of carcasses on which a particular taxon was occurred.

Taxa Number per carcass:	Range	Mean
Ephemeroptera		
(n= 4) Heptageniidae-*Cinygmula*	1-30	(9)
(n=2) Heptageniidae-*Ironodes*	1-2	(1.5)
(n= 5) Baetidae-*Baetis*	1-51	(24)
(n=4) Ephemerellidae-*Drunella*	1-2	(1.5)
(n=2) Ephemerellidae-*Ephemerella*	1-25	(13)
Plecoptera		
(n=11) Nemouridae-*Zapada*	1-30	(28)
(n=2) Chloroperlidae-*Alloperla*	1-5	(3)
Trichoptera		
(n=5) Limnephilidae-*Apatania*	1-4	(3)
(n=2) Limnephilidae-*Dicosmoecus*	4-10	(7)
(n=12) Limnephilidae-*Ecclisomyia*	4-1000+	(100)
(n=6) Limnephilidae-*Hydatophylax*	2-14	(6)
(n=1) Limnephilidae-*Nemotaulius*	4	(4)
(n=18) Limnephilidae-*Psychoglypha*	1-350+	(56)
(n=4) Brachycentridae-*Brachycentrus*	1-15	(4)
(n=4) Glossosomatidae-*Glossosoma*	1-6	(3)
(n=1) Rhyacophilidae-*Rhyacophila*	1	(1)
Diptera		
(n=15) Chironomidae	1-400+	(51)
(n=5) Simuliidae-*Prosimulium*	1-62	(16)
Turbellaria		
(n=5) Tricladida	3-87	(26)
Arachnoidea		
(n=1) Trombidiformes: Hydracarina	1	(1)

anadromous fish include fry of rainbow trout, grayling, king and silver salmon and sculpins (*Cottus cognatus*). Other large vertebrates include black and grizzly bears (*Ursus americanus, U. arctos*), grey jays (*Perisoreus canadensis*), mew and glaucous-winged gulls (*Larus glaucescens, L. canus*), ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), marten (*Martes americana*), mink (*Mustela vison*) and river otter (*Lutra canadensis*). Some entrainment appeared essentially permanent when carcasses downstream of large stream structures (rocks and logs) are covered with shifting sand and gravel (Figure 2.6). These rotting carcasses are then readily available for undisturbed use by microbes and streambed-dwelling macroinvertebrates, including oligochaetes. Aquatic oligochaetes, extremely rare in all study streams, were only collected in those stream stretches containing numerous entrained salmon carcasses (≥ 1 per m of stream length).

Fluctuating water levels eventually free most carcasses: simultaneously and intense, internal microbial activity during initial entrainment sets the stage for the next step in carcass disintegration. Newly released carcasses are buffeted and twisted by stream turbulence while bouncing off rocks and other debris. These carcasses commonly burst apart as their once tough, but now microbially weakened skin splits open. Decomposing and partially liquified muscle tissue along with surprisingly intact viscera commonly spill out of the skin, settling into the flow's boundary layer next to the benthos (Figure 2.7). Here, wide dispersion and small particle size facilitates rapid use by all stream biota. My study of chum-salmon decomposition rates (see following section) showed that carcasses near this state of deterioration prior to disintegration

Figure 2.6. Chum salmon becoming esconced in stream benthos.

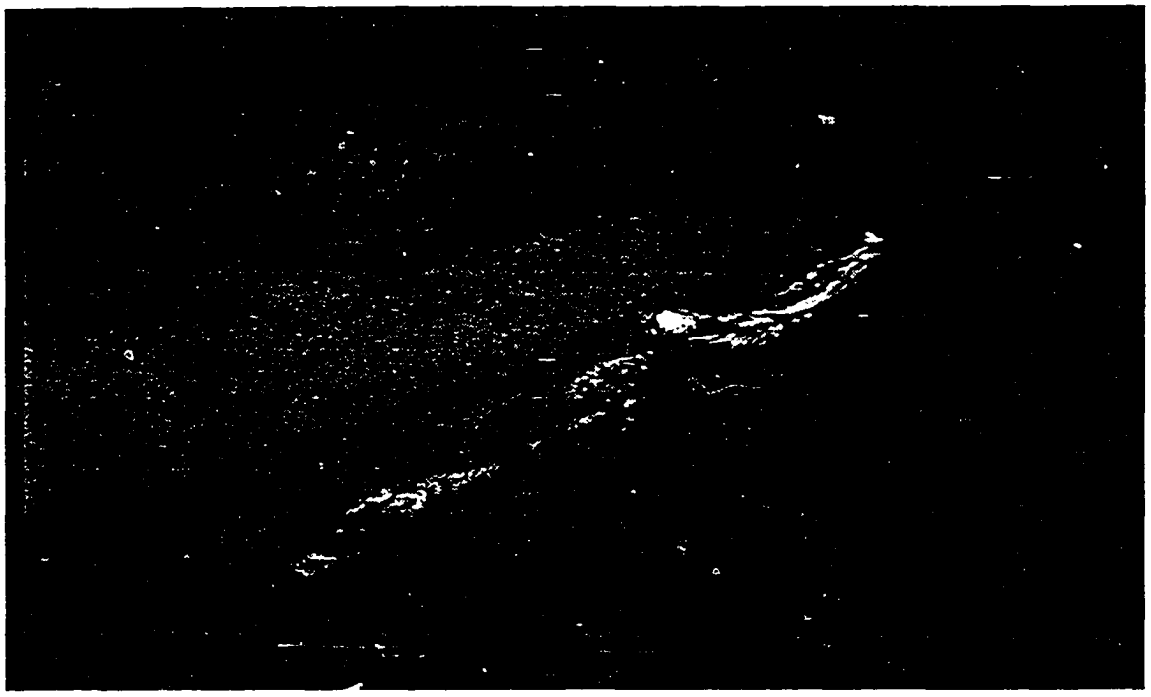
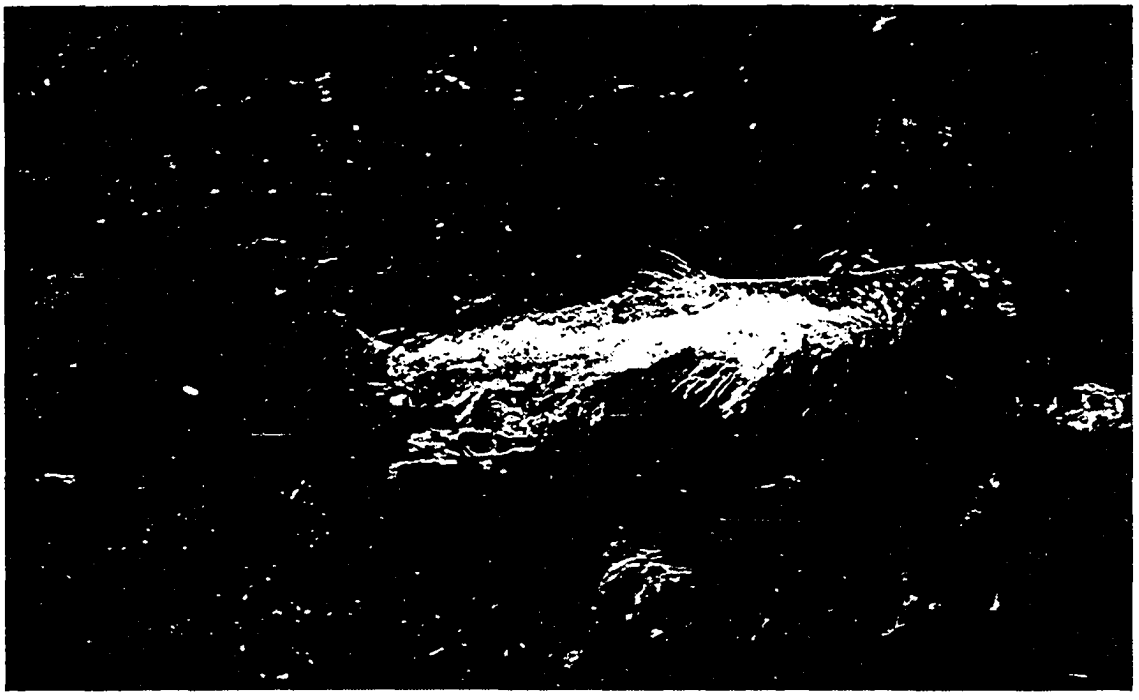


Figure 2.7. Salmon carcass disintegrating in stream turbulence. Small pieces of flesh settle into the boundary layer making for easy utilization by stream macroinvertebrates.



still retained 50% of original dry biomass. Fish skins and bones settle out also but are slower to decompose; bones may last several months or longer. No further downstream movement of salmon body parts is likely outside of flood events that include stream-bed movements.

Macroinvertebrate use of salmon

Salmon carcasses or their parts examined in and along streams invariably had macroinvertebrates on them. Macroinvertebrate communities in streams are dynamic feeding assemblages (Cummins and Klug 1979). Many taxa display an annual life-history pattern with a nonfeeding pupation period that can last several months or more. Almost all stream macroinvertebrates leave the stream upon emergence, living terrestrially for a variable period. Given this underlying pattern, the likelihood that any particular taxon will be present on carcasses at a particular time depends upon the organism's life history pattern. For example, late instar *Psychoglypha* (Trichoptera: Limnephilidae) were commonly occurred on carcasses during July and early August but were absent in September after their typical late summer emergence. Other trichopterans emerge in May and June so their larval stages are not common until late August and September. Nymphal plecopterans, (Nemouridae-*Zapada*), were absent from stream food webs from June through August during their terrestrial adult and aquatic egg stages, but became common in late September and October when eggs hatched and early instar nymphs typically focused on energetic inputs from leaf fall.

Most lotic insects, rather than just reacting to carcasses as stream structure to explore, were localized in distribution on the carcass. They positioned themselves either on exposed flesh (skin not present) or in the

thick fungal growths common to most carcasses. Only blackflies (Diptera: Simuliidae-*Prosimulium*) appeared to position themselves for optimum exposure to stream flow rather than away from current and near abraded salmon flesh. Low-profile turbellarians occurred anywhere on a carcass including positions exposed to stream flow. The only instances observed where no aquatic macroinvertebrates were present were on carcasses flushed from spawning streams into channels of glacial streams. High silt loads, frequent streambed movement and silt substrate apparently preclude a significant or stable lotic macroinvertebrate community at such sites.

Colonization of salmon carcasses was rapid. For example, on two occasions, freshly killed salmon were put back into 0.5-m deep runs of Troublesome Creek and secured to the streambed. These carcasses were retrieved within 2 hours of placement. All common macroinvertebrate taxa found in the stream, except for net-spinning caddisflies, were on the carcass at that time. Typically, macroinvertebrate taxa cluster in mouth and gill areas of fish in fast currents (Figure 2.8) and abraded body parts (tails, fins, eyes, nose) of fish in slow current (Figures 2.9 and 2.10). They appear to feed on gill membranes or mucosa in the oral cavity as well as exposed muscle in the abraded areas and fungal patches on nonabraded parts of fish. In all but the slowest water, most invertebrates positioned themselves beneath the carcasses, probably for protection from current if not from predators. In still waters, where current effect is negligible, carcasses or parts of carcasses (Figure 2.11) were seen nearly covered with caddisflies. Over 1,000 midinstar caddisflies (Trichoptera: Limnephilidae-*Ecclisomyia* and *Psychoglypha* occurred on one salmon head (Figure 2.12). Their biomass represented a

Figure 2.8. Lotic macroinvertebrates feeding in gill cavity of dead king salmon.This area, free of current and possessing soft flesh, is immediately targeted.

Figure 2.9. Lotic macroinvertebrates on abraded tail of salmon carcass. The often The often abraded tail of dead salmon offers purchase and exposed flesh to stream macroinvertebrates.

Figure 2.10. Stream macroinvertebrates focus on abraded areas on head of salmon. Exposed flesh and an empty eye socket provided food and refugia.

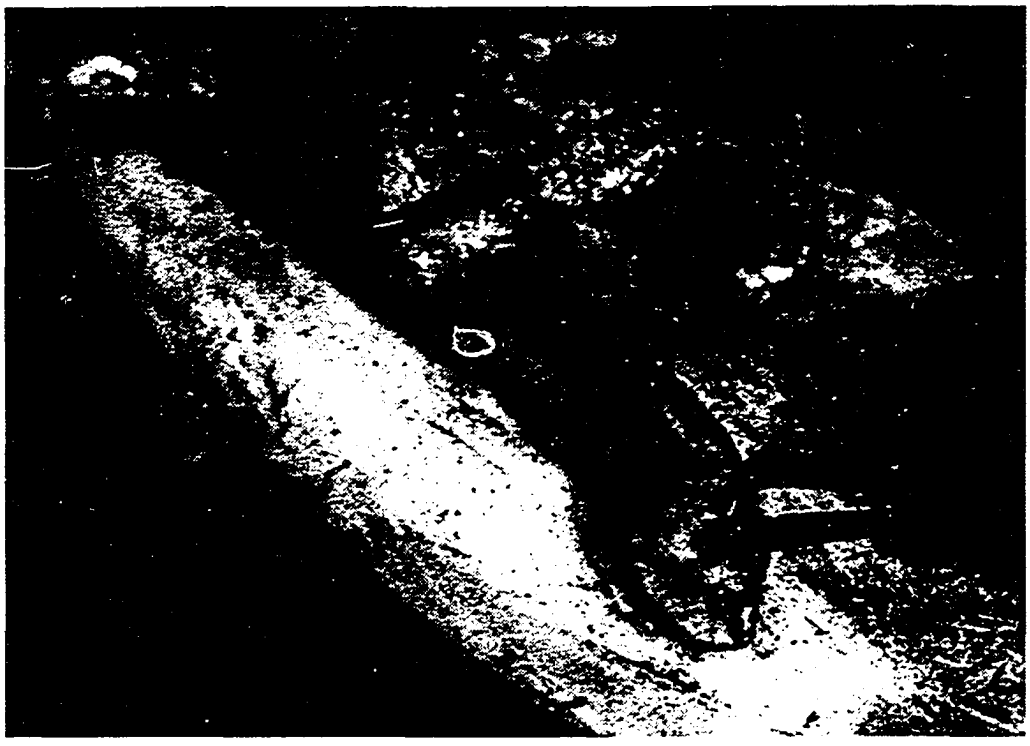


Figure 2.11. Caddisflies (Trichoptera: Limnephilidae-*Psychoglypha)* cluster on salmon milt sacs in a slow-moving section of stream.

substantial fraction (≥10%) of the weight of their food. Usually the biomass of lotic macroinvertebrates feeding on a whole carcass is many orders of magnitude less than the biomass of the whole carcass.

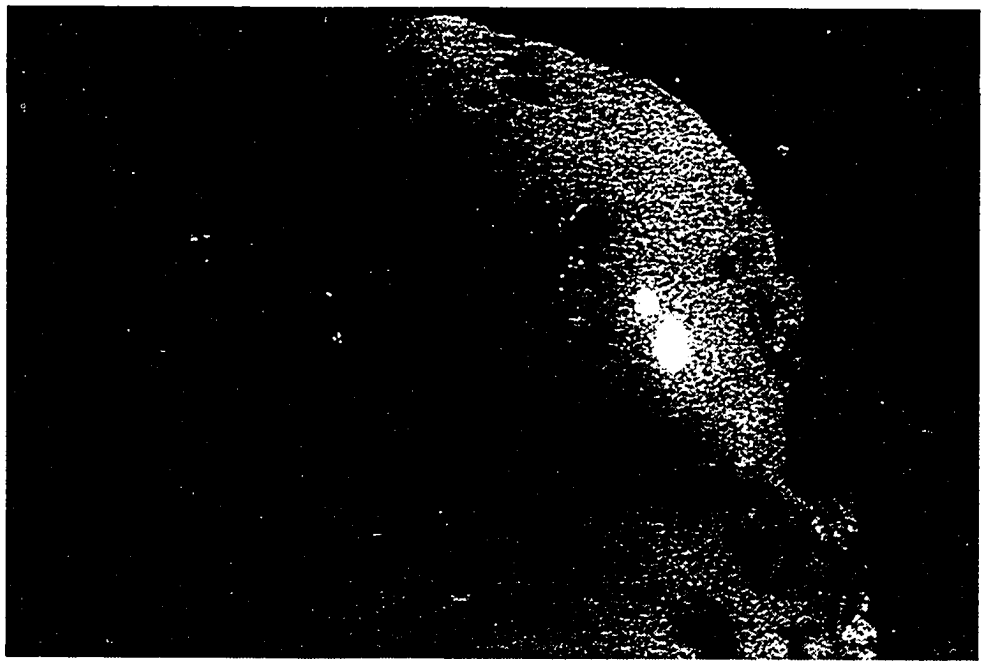
Except for the aforementioned incident of caddisflies covering a fish head lying on the benthos, there was little evidence that lotic macroinvertebrates play a regular role in facilitating decomposition of salmon carcasses by cutting through the skin into the body cavity and so aiding entry of microbial decomposers. Only one instance was noted during the study where a lotic macroinvertebrate (Trichoptera: Limnephilidae-*Ecclisomyia*) actually burrowed into and was mostly immersed within the flesh. In this instance, the flesh was a relatively small and soft milt sac of a salmon (Figure 2.13) rather than the tough skin on a large carcass. Thus, aquatic macroinvertebrates, while consistently present on carcasses, did not appear to contribute significantly to the mechanical disintegration of those carcasses.

One king salmon carcass was casually examined three times throughout its decomposition during July-August 1988. These periods were recent death, moderately progressed decay, and advanced deterioration. *Psychoglypha* (Trichoptera: Limnephilidae) was the dominant taxon on the carcass. No orderly progression of different lotic taxa utilizing this carcass as it decayed was observed.

On two occasions, rotting salmon carcasses were placed into slow, shallow sections of Troublesome Creek. They were then observed for approximately 1 hour. Though visibility through the water was poor for seeing small macroinvertebrates, large caddisflies (Trichoptera: Limnephilidae-*Psychoglypha*) were observed coming to the carcass from ≤ 1

Figure 2.12. Concentration of caddisflies on head of salmon. This salmon head located in a slow moving section of stream had over 1000 caddisflies (Trichoptera: Limnephilidae-*Ecclisomyia* and *Psychoglypha*) feeding on it.

Figure 2.13. Caddisflies boring into milt sac. *Ecclisomyia*, (Trichoptera: Limnephilidae), were the only stream macroinvertebrates noted that penetrated flesh rather than just fed superficially.



meter away. They appeared to feed for short periods (<15 min) before leaving. Whether feeding visits by individual caddisflies were repeated and, if so, how often was not determined. The universality of this visitation behavior in other stream taxa is unknown.

On one occasion, a net-spinning caddisfly (Trichoptera: Hydropsychidae *Arctopsyche*) located in riffles below a fish cleaning area on Byers Creek, was observed trying to pull a 2 cm by 1.5 cm piece of salmon liver (>three times larger than itself) into its net.

On two occasions, blowflies found and laid hundreds of eggs on a fresh dead salmon within 15 minutes of exposure to the atmosphere. This occurred despite a noticeable absence of blowflies before exposure of the salmon carcass, cloudy skies and cool temperatures (<7°C). Blowfly eggs were common in the gill chambers of salmon left exposed to air in shallow riffles (Figure 2.14). Eggs developed into large larvae within 3 days when temperatures ranged from 5°C to 10°C. Larva feeding on exposed carcasses commonly washed off when rising water levels resubmerged the carcass (Figure 2.15). On seven occasions, dead blowfly larva were on submerged carcasses while live blowfly larvae were found on submerged carcasses only twice. Blowfly larva used all available flesh from one 15+ kg salmon carcass left on a gravel bar <8 days (Figure 2.16).

Use of carcasses by fish, birds, and animals

On many occasions during July and August 1988, fry of coho salmon (5 cm to 7.5 cm) were seen feeding on salmon carcasses, tugging mightily on exposed muscle filaments. Because many carcasses settled into slow waters where salmon fry abounded, fry in large numbers may greatly enlarge abraded

Figure 2.14. Blowfly eggs in gill chambers of carcass exposed to air. *Brachycentrus* present also.

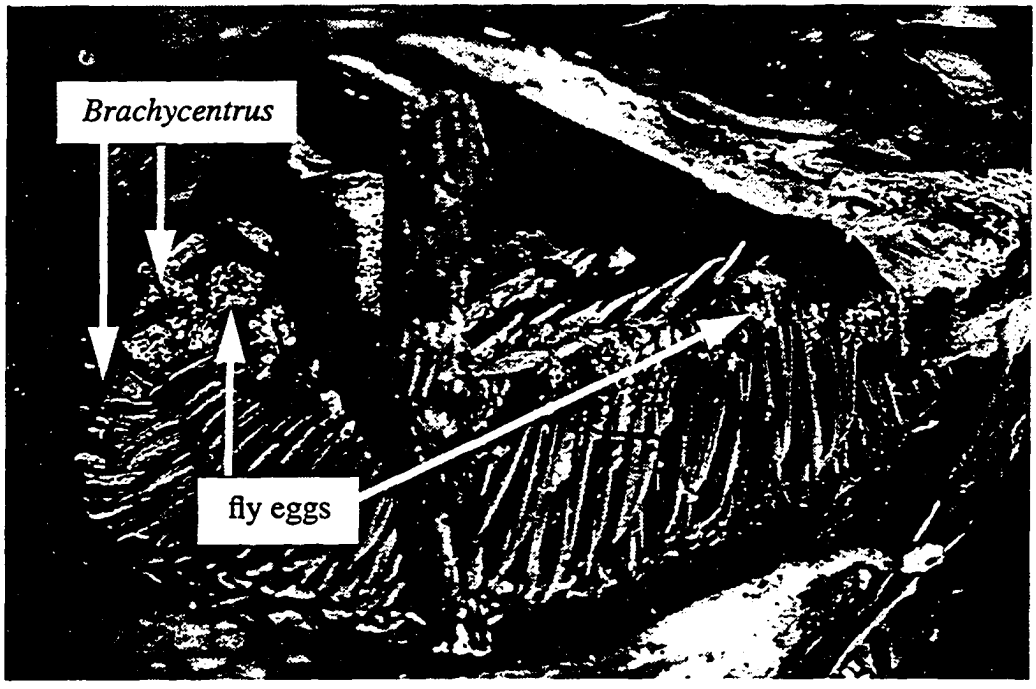


Figure 2.15. Blowfly larvae on king salmon carcass stuck on riffle. Blowfly larva (Diptera: Calliphoridae) have hatched and are quickly consuming exposed carcass.

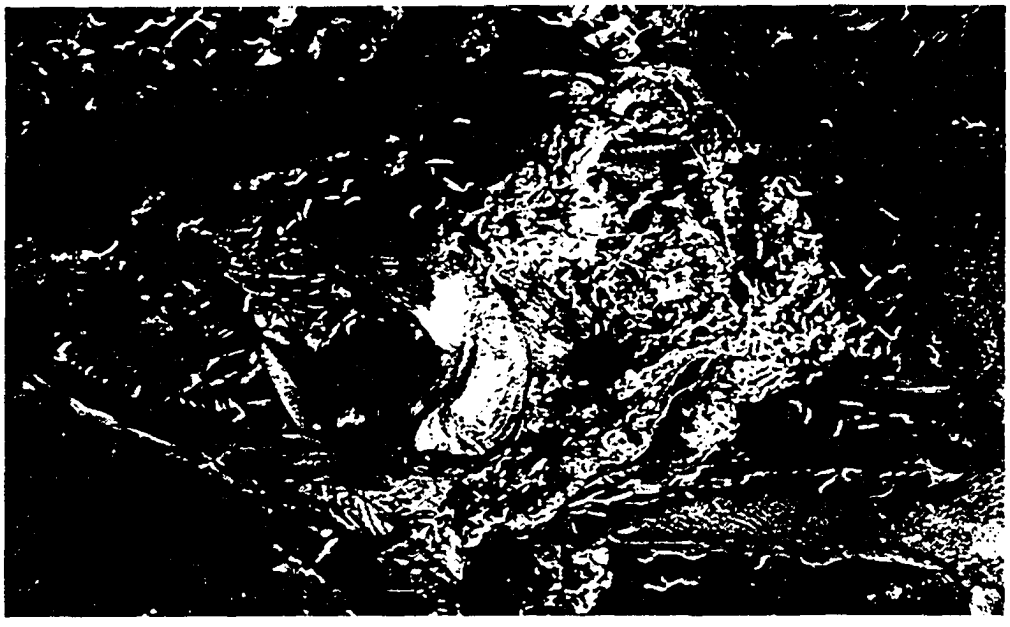


Figure 2.16. King salmon killed by bears and left to blowflies. The blowfly (Diptera: Calliphoridae) larva pictured here reduced the carcass to bones in less than eight days.

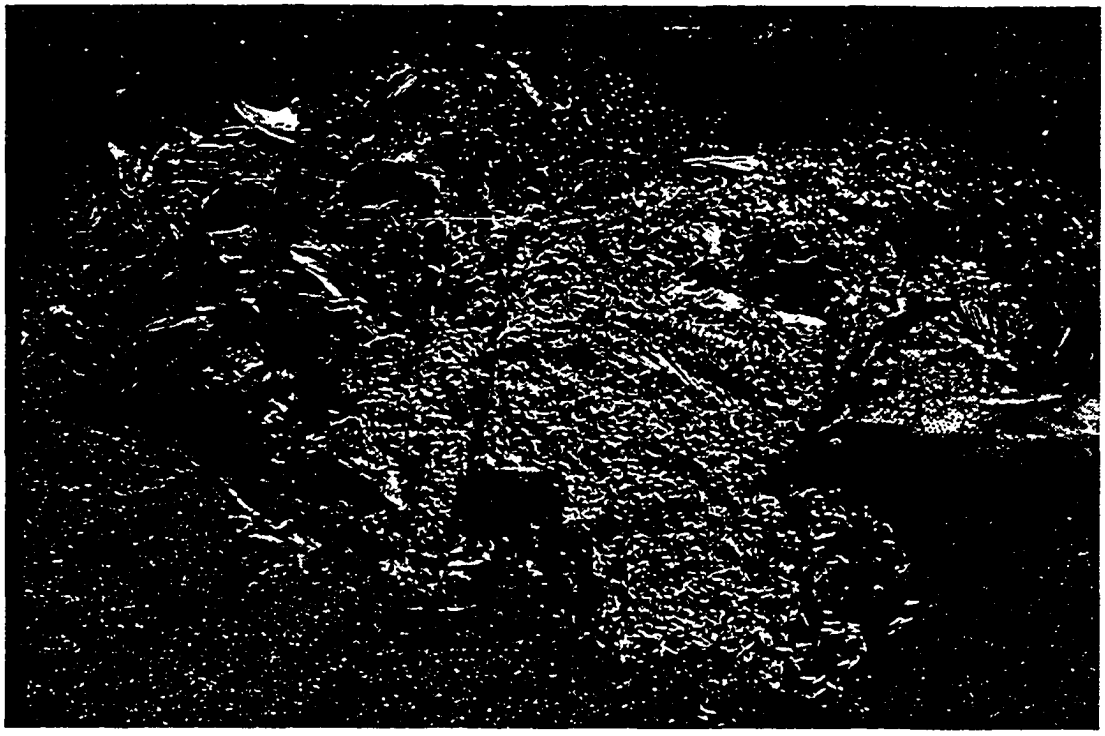
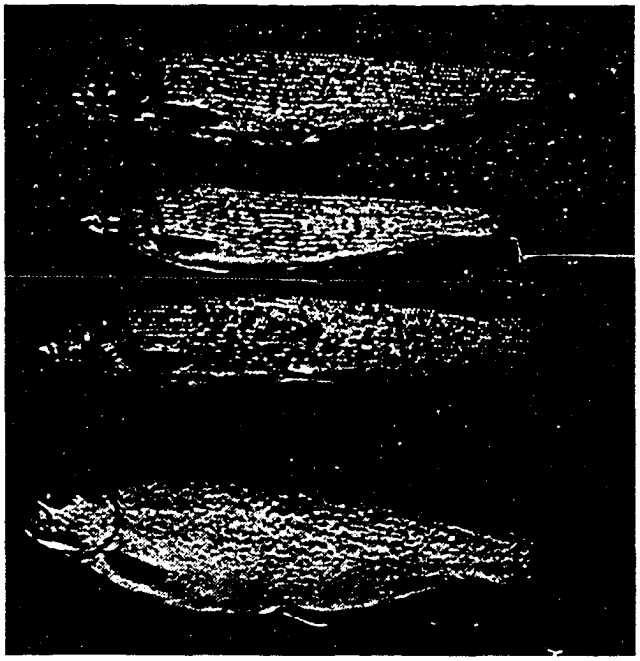


Figure 2.17. Grayling and rainbow trout caught below a salmon spawning area. They were feeding exclusively on lost salmon eggs. Note the greater apparent success of the rainbow trout.



areas on carcasses, significantly contributing to salmon carcass disintegration. One sculpin was observed in a similar feeding activity. Although less easily observed than salmon fry, sculpin were more common in spawning areas and may contribute significantly to carcass deterioration. A heavy density (est. $15^{+} \cdot m^{-2}$) of sculpin was observed in riffles below a concentration of salmon carcasses on Clear Creek in October 1993 compared to a usual observed density of $<1.0 \cdot m^{-2}$.

Casual field examination of stomach contents from approximately 3 dozen rainbow trout throughout the ice-free season in 1988 through 1993 showed a predictable cycle in diet. During May and June, rainbows focused on emerging chum and pink salmon fry when available. Otherwise, the main prey was large, late instar caddisflies and mayflies. After salmon arrived and spawning commenced, rainbows were observed on numerous occasions stationing themselves below spawning salmon gorging on lost eggs with apparent effects on body condition (Figure 2.17). During 1988, rainbows so targeted abundant eggs that large congregations of coho fry were completely ignored as they were not found in rainbow stomachs. In 1993, numbers of spawning salmon were extremely low in Pass Creek. Then, large stream macroinvertebrates made up the bulk of rainbow diet though stomachs of five of six rainbows killed during August contained one or more salmon egg-like soap berries (*Sheperdhia canadensis*). Though salmon flesh was found in only two of all rainbow trout captured, a fishing lure mimicking a piece of fungus-covered salmon called the 'flesh fly' (a strip of rabbit skin including fur tied to a #12 hook) was effective at catching them.

The seasonal diet cycle of grayling is similar to that of rainbow trout.

They target salmon fry in the spring and salmon eggs when available. In dozens of observations, rainbows out-competed similar-sized grayling for salmon eggs when both fish are present. During my study of salmon carcass decomposition rates (following section), only grayling were present. One dozen to three dozen grayling positioned themselves below me whenever I removed a carcass from the streambed. They appeared to target small particles of salmon flesh that were flaking off during carcass retrieval. No obvious salmon flesh was actually discerned in any of dozens of grayling stomachs examined over the course of the study from streams in Denali State Park though salmon eggs were common.

Field examination of stomach contents from eight longnose suckers (*Catastomus catastomus*), collected in Byers Creek during August of 1988 (3), 1990 (3), and 1993 (2) showed flesh from fragmented salmon was the dominant dietary item of these fish, with a wide range of common stream macroinvertebrate taxa comprising the remainder of the stomach contents. It appears these longnose suckers fed on chunks of flesh from disintegrating salmon, a divergence from their normal diet of algae, plants and detritus (Morrow 1980).

Four dippers collected in salmon streams during September 1988 all had pieces of salmon tissue in their stomachs. During June of 1994, two dippers were observed diving into Haley Creek (a tributary of the Copper River approximately 16 km south of Chitna, Alaska). They targeted a section of stream below a fish cleaning area and were retrieving chunks of salmon flesh, eggs and offal off the stream bottom. These food items were taken ashore before being either fed to juvenile dippers or eaten.

Little use of salmon carcasses by other birds was noted. Only once was a bald eagle seen feeding on a carcass. Despite regular evidence of gulls and ravens feeding on carcasses (tracks in the sand and eyes pecked out of carcasses), they were rarely observed doing so.

Both black bear and grizzly-brown bears regularly took and ate both live and dead salmon from the study streams. Eating of the salmon usually did not take place at stream-side but most commonly occurred 5 m to 25 m away from the stream on heavily vegetated banks. Typically, the flesh, gonads and most of the head were eaten with the offal, backbone and gills left behind. Even in prime feeding areas, each fish taken by bears was eaten at a different location: no feeding stations where bears would continually return to eat their catch were noted. During a particularly heavy period of a king salmon run on Pass Creek in 1988, grizzly bears left 38 fish uneaten on the bank. These incompletely spawned fish amounted to ≈3% of the estimated salmon run in this stream. There may be a significant fertilizing effect on riparian zone vegetation from transport of salmon by bears (whole fish, partially eaten carcasses, or as feces) as riparian zones along salmon streams often seem more lush and green.

Heterotrophs and moss in salmon streams

A sewage fungus complex (SFC) commonly occurred in Byers Creek, Lower Pass Creek and Lower Troublesome Creek from Autumn 1987 until spring 1989. No attempt was made to identify the components of the SFC. SFC is commonly composed of different taxa of filamentous algae, filamentous bacteria, and fungi (Esho and Benson-Evans 1983). SFC decreased in abundance during April 1988 and 1989 but waxed during the king salmon run (June) in 1988. Maximum covering of the stream bed by the SFC occurred just

after the peak of salmon spawning activities (September/October) that year. In stretches of Byers Creek, the SFC then appeared thick enough (5 to 7.5+ cm) to limit formerly heterogeneous benthic habitat. After its disappearance in April 1989, the once widespread and extensive SFC did not recur. Record spring runoffs, unusually high summer precipitation and apparently lower salmon runs over the next several years are suspected causal factors.

Aquatic moss occurred on an estimated 30% of all substrates >30 cm in all salmon-enriched systems at start of this study. This moss disappeared after several years of apparent lower escapement and regular high-water conditions.

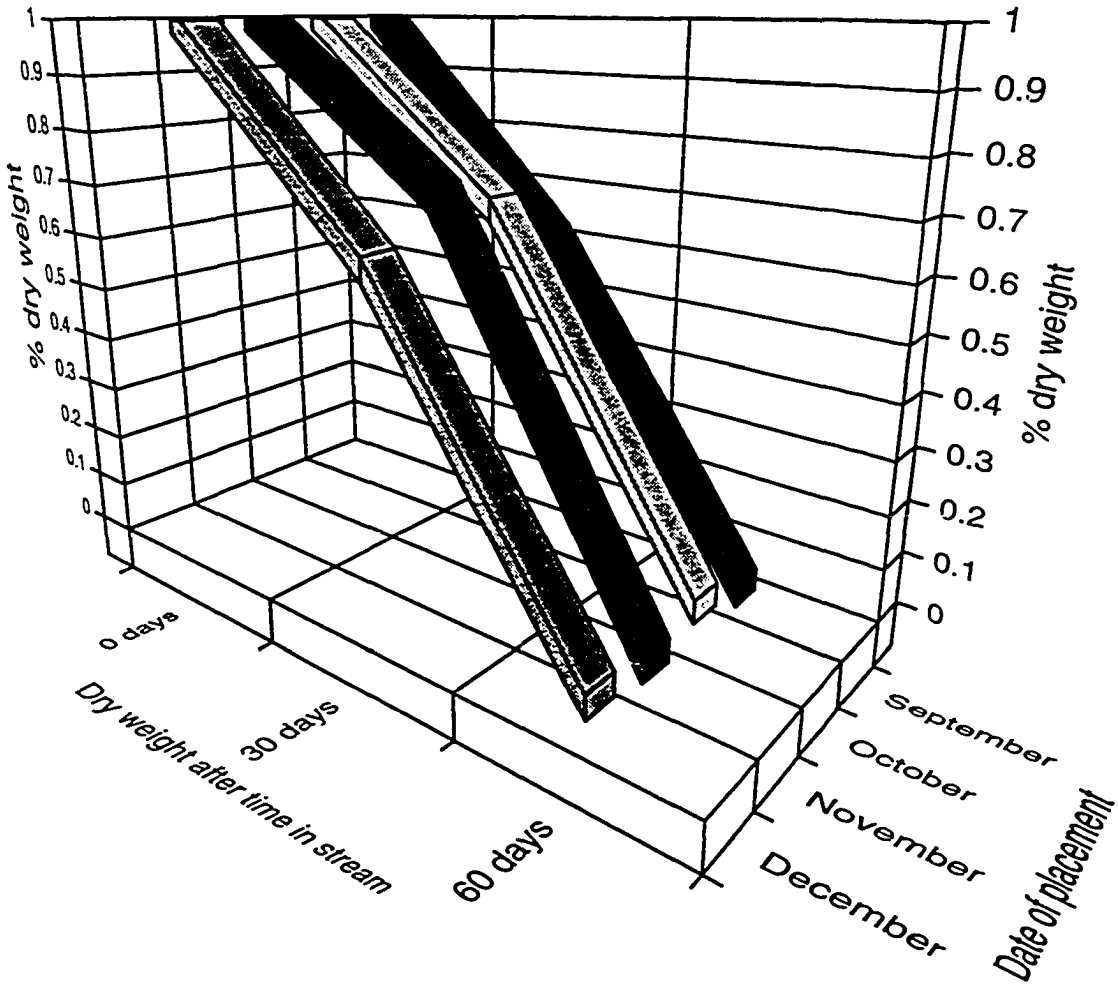
Rates of salmon carcass deterioration

The average dry weight of whole, pre-spawned chum salmon was 29% (n = 2) and 23% (n = 3) of fresh weight for females and males respectively. After 1 month of decomposition in Clear Creek, all fish recovered were covered with a >1 cm thick fungal mat. The fungal mat was not removed from these carcasses before drying and weighing for fear of rupturing skin and losing internal liquified muscle tissue. Including the weight of this fungal mat, females had lost an average of 40%±SD (n=4) of estimated original dry weight while males lost an average of 35%±SD (n=4) (Figure 2.18). After 2 months of decomposition in Clear Creek, only bones and shreds of skin remained from all fish. Females lost an average of 97% (n = 2) of estimated original dry weight while males lost an average of 95% (n = 9).

DISCUSSION

The potential importance of anadromous fish carcasses in

FIGURE 2.18. Average decomposition rates (% dry weight remaining) of chum salmon (Onchorhynchus keta) carcasses placed monthly in Clear Creek near Anderson, Alaska from September through December 1993. Shaded bars indicate dry weight loss of carcasses placed in streams at the beginning of each month.



nutrient-limited stream ecosystems is well-documented (Durbin et al. 1979 ; Kline et al. 1989; Rand et al. 1992; Richey 1975). Supporting these findings, both Cederholm et al. (1989) and Glock et al. (1980) found that most carcasses in study streams in Washington remain in the general spawning areas despite significant flood events. Carcasses were used by terrestrial biota, directly providing energy and nutrients. While information about the importance of salmon carcasses to maintaining terrestrial populations of omnivore is limited (Fisher 1890; Hansen 1987), an interior Alaska subsistence user stated "there are more animals on the land, birds in the trees and fish in the streams during and after large salmon runs" (Doug Sweat, subsistence user, Kaltag, Alaska, pers. comm.). Despite the potential importance of salmon carcasses in supplementing aquatic food webs, there have been no studies of the actual physical processes by which salmon carcasses enter stream food webs.

Salmon carcasses commonly were retained in spawning areas of the Alaska noncoastal streams I studied. This retention occurred despite relatively high gradients and generally low biomass of large woody debris. Local capture of salmon nutrients appears to rely on a 'disassembly line' of microbes, invertebrates and fishes. Successful retention of nutrients by a stream system requires rapid use of carcasses before periodic flood events carried carcasses downstream.

Although present on almost all carcasses, aquatic macroinvertebrates were usually not important in initial carcass deterioration. As Minshall et al. (1991) reported, initial fish decomposition appeared to be primarily microbial. But when hydrologic conditions (slow moving water) occurred, lotic

macroinvertebrate use of intact carcasses may be comparable to that found terrestrially. Such incidents, akin to those observed by Brusven and Scoggin (1969), were noted but were not the rule. Taxa they found important (Trichoptera: Limnephilidae-*Dicosmoecus, Ecclisomyia* and *Psychoglypha*) in the rapid disintegration of squawfish (*Ptychocheilus oregonensis*) in northern Idaho were also consumers of Alaskan salmon carcasses. But regardless of whether macroinvertebrates are initially important in opening and consuming salmon, once microbes weaken the skin and carcasses fragment into many small pieces, macroinvertebrates can directly consume this animal FPOM and so reap a direct energetic and nutrient benefit, with consequences for higher trophic levels.

Salmon fry, sculpin, and rainbow trout can be significant consumers of both salmon carcasses and certainly the macroinvertebrates that feed on carcasses. Thus fitness of silver and king fry may relate directly to the food availability (salmon run size) during their first summer post-hatching. Riparian-zone and stream-dwelling birds may be effected by salmon run strength. For example, dippers and harlequin ducks (*Histrionicus histrionicus*) both depend on stream invertebrates for food. The number of these birds on my study streams appeared to drastically decline (based on casual observation during the course of my study, paralleling decreases in salmon escapement. A causal relationship has not been established but warrants further study.

No measurements of salmon decomposition rates were kept during summer 1988 although most salmon carcasses completely disintegrated much faster (<1 month) than in later years. I speculate that the sewage fungus complex present in 1988 reflects both storage of previous organic inputs (i.e.,

salmon carcasses) and provides a reservoir of microbes involved in carcass decomposition and trapping of organic-matter inputs. Thus, a loss of this reservoir may result in slower rates of salmon decomposition and a lowering of stream efficiency at retaining marine-derived nutrients and energy.

Bowden et al. (1994) showed that several species of moss present in a tundra stream proliferated after experimental phosphorus additions to the stream. Thus, some mosses in streams may be dependent on and function to trap the nutrients provided by large numbers of salmon carcasses. The structure of moss, known to retain allochthonous detritus while providing structure for autochthonous production by periphytic algae (Bowden et al. 1994), may also serve to physically retard carcass loss from the system while further functioning as habitat for macroinvertebrates that use salmon carcasses. Moss abundance declined during the course of the study again paralleling decreases in salmon escapement. Flood events, short of cobble moving torrents, are thought to have slight effect on epilithic bryophytes (Bowden et al. 1994; Englund 1991).

Actual deterioration of salmon carcasses specifically placed in spawning streams during this study was rapid compared to measured rates of decomposition of rainbow trout placed in nonanadromous stream in Idaho (Minshall et al. 1991) and red salmon placed in a nonanadromous stream in Alaska (Kyle and Koenings unpublished). In Idaho, trout carcasses averaging ≈100 gm required 120 days to decompose while spawned-out red salmon carcasses averaging 2.5 kg required up to 90 days to decompose. In this study, chum salmon, averaging 2.5 kg, decomposed in under 60 days despite cooler water temperatures (> 4°C versus ≈ 0°C). This suggests that anadromous

salmon streams develop a microbiota able to efficiently use salmon carcasses, similar to the microbial floras adapted to use terrestrial inputs (leaves) during the Autumn. There was little change in rate of decomposition between fish placed in early September (water temperature ≈2°C) and October through December (water temperature ≈0°C) when biological activity is normally thought to be slow (Figure 2.18).

In Alaskan rivers and streams, biotic and abiotic mechanisms clearly exist for capture and retention of seasonally available salmon carcasses. Spawning streams may serve as highly productive and diverse oases within an oligotrophic subarctic environment. The nutrient input required for a stream to sustain the biotic constituents necessary for such a self-enhancing system is unknown. Commercial fishing overharvest and sport fishing on spawning grounds can diminish small runs, resulting in even smaller runs and in destabilizing positive feedback rippling through higher trophic levels within the watershed. Given the apparent ease by which carcasses are retained in streams, their importance in biogeochemical cycling should be incorporated into strategies for fisheries management. Future salmon biologists may have to manage salmon runs for both number of spawners (eggs) and for carcasses (nutrients and energy) needed to sustain highly productive rearing environments for both anadromous and nonanadromous fishes.

Chapter 3-Macroinvertebrate community response to enrichment in southcentral Alaskan streams

INTRODUCTION

The community structure of benthic macroinvertebrates in the streams and rivers of interior and southcentral Alaska is less complex than that in temperate climes. Diptera, Plecoptera and Ephemeroptera dominate in Alaska running waters whereas Trichoptera are uncommon and many other orders are rare or absent (Oswood 1989). An apparent exception occurs in streams that either receive runs of Pacific salmon (*Oncorhynchus* spp.) or have lake outlets as sources. In these systems, many Trichoptera taxa are at least occasionally present with one net-spinning Family, Hydropsychidae, occasionally common or abundant. Pianka (1978) and Southwood (1966) have suggested that large increases in food inputs to a system would potentially increase abundance and complexity of the community as long as spatial heterogeneity is maintained or increased. Both marine-derived nutrients from salmon runs and seston-rich lake discharge constitute such additions. Further research into this phenomenon in headwater systems in Alaska is important because: (1) salmon streams and lake outlets constitute "natural experiments" (Kline et al. 1989; Richardson and Mackay 1991) in understanding the roles of biotic factors in structuring stream communities (Koetsier 1987); (2) streams and rivers enriched with marine nutrients or lake seston may serve as highly productive and diverse oases within an oligotrophic subarctic environment; and (3) such research will provide data on ecosystem function, aiding decision-making processes in resource management (e.g., sport-commercial-subsistence fishing, mining, forestry,

recreational development).

While most recent research in stream ecology (specifically energetics) focuses on the relative importance of allochthonous inputs (leaves and other plant parts from streamside vegetation) versus autochthonous inputs (algae and macrophytes) into headwater streams (Cummins 1974, Minshall 1978), studies investigating the linkage between the marine environment and freshwater ecosystems indicate marine nutrient input may also be important (Brickell and Goering 1970; Donaldson 1967; Kline et al. 1989; Juday et al. 1932; Richey et al. 1975). Increased nutrients from spawning of anadromous fishes may result in cascading ecosystems effects, including greater primary production, heterotrophic production, and enhanced decomposition of leaf detritus (Durbin et al. 1979, Richey et al. 1975, Spencer et al. 1991).

Annual runs of various Pacific salmon species, chum/dog (*O. keta*), king/chinook (*O. tschawytcha*), pink/humpy (*O. gorbuscha*), red/sockeye (*O. nerka*), and silver/coho (*O. kisutch*), provide a dependable source of energy, protein, and inorganic nutrients (e.g., P, N) for microbes, aquatic insects, terrestrial birds and animals. Increased energy inputs likely would increase abundance and production of all aforementioned organisms (Pianka 1978), although two past investigations suggests otherwise. Hildebrand (1971) found substrate disruption by spawning salmon led to both a decrease in density and a change in community structure of benthic invertebrates. Ruggles (1959) noted that a 10-fold increase in rearing salmon fry led to an 80% decrease in the bottom fauna apparently via predation by fry on macroinvertebrates.

Extremely high density of filter feeders at lake outlets in temperate

climates is a well-documented phenomenon (see Richardson and Mackay [1991] for review). Densities are highest at the outlet and decline precipitously downstream. (e.g., Briggs 1948; Maciolek and Tunzi 1968; Oswood 1979; Valett and Stanford 1987). In their review, Richardson and Mackay (1991) argue that past studies indicate certain lake-mediated factors, abundant and high quality food (seston), stable temperature and flow, couple with typical upstream flight of gravid females to work in concert contributing to the high concentration of macroinvertebrates. Density of filterers downstream from the lake outlet declines as macroinvertebrates at the outlet efficiently remove virtually all lake-derived seston from the water. How conditions common to Alaska, e.g., reduced to nonexistent flow during long winters and the often significant disturbance to the benthos from ice-break in the spring (Scrimgeour et al. 1994), would change the lake outlet effect.

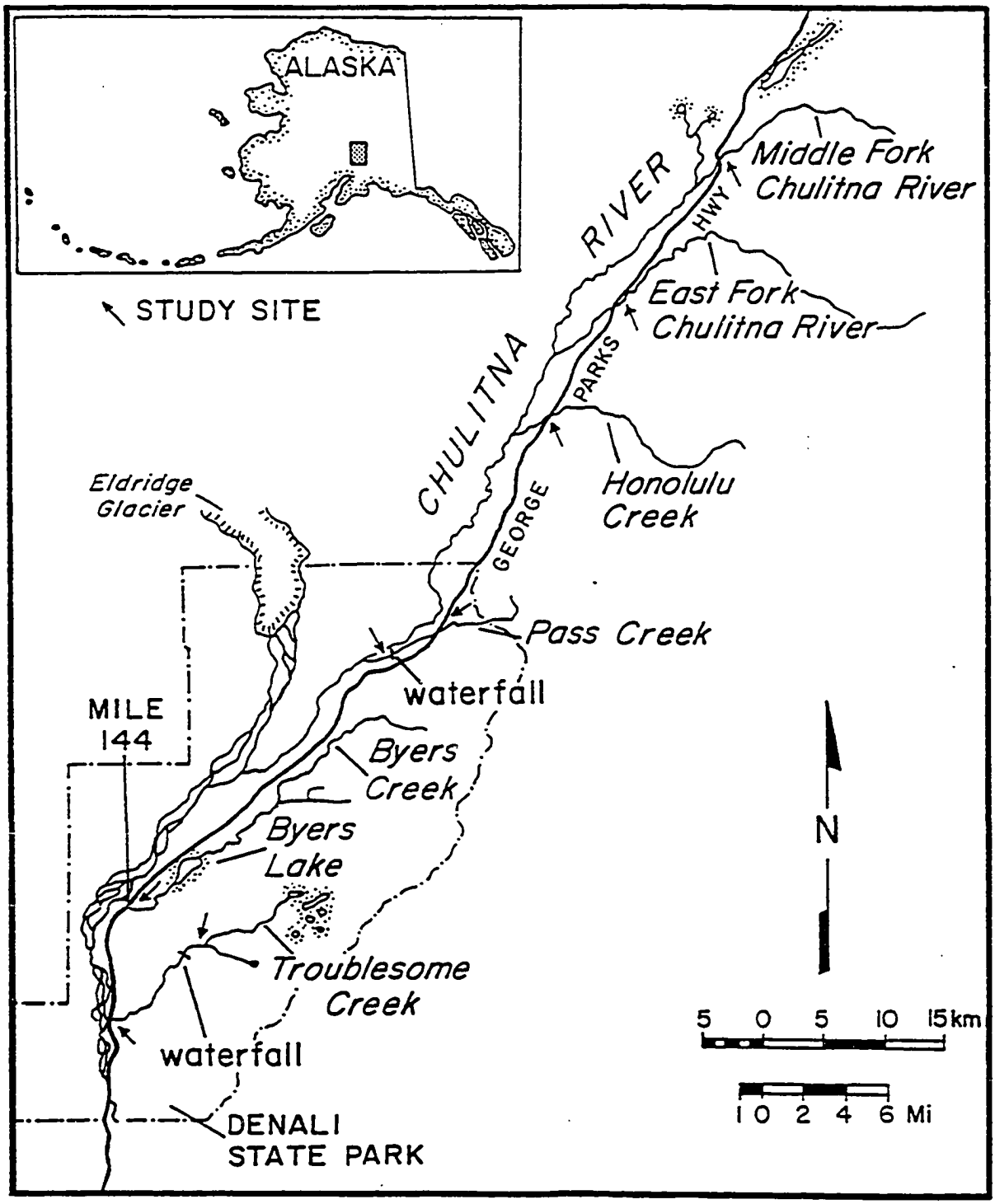
The specific objectives of this study were to identify taxa and functional groups of taxa in southcentral Alaska streams receiving enrichment either from salmon runs or lake outlets or both, and to test the hypothesis that enrichment from these sources has a discernible effect on stream macroinvertebrate community structure in this oligotrophic, subarctic environment.

METHODS AND MATERIALS

Study sites

The study streams are located approximately 140 km NNE of Anchorage in southcentral Alaska (Figure 3.1). Located south of the Alaska Range, they drain the Talkeetna Mountains and flow into the Chulitna River. The Chulitna River in turn, flows into the Susitna River, which flows to

FIGURE 3.1. Map of Chulitna River drainage in southcentral Alaska. Insert locates position of region in Alaska. Sampling site locations on each study stream are delineated by arrows (➡).



Cook Inlet and the North Pacific Ocean. All sampling sites were chosen for accessibility from the George Parks Highway. The 1988 study sites were Lower Troublesome Creek, Upper Troublesome Creek, Byers Creek, Lower Pass Creek, Upper Pass Creek, and Honolulu Creek. The 1990 season included sampling additional nearby drainages; the East Fork of the Chulitna River and the Middle Fork of the Chulitna River.

The climate of the area is maritime, with the Alaska Range to the north trapping warm moist air coming from the North Pacific Ocean. Seasonal precipitation can exceed 125 cm water equivalent with snowfalls of >9 m not uncommon (R. Ostermick, Ermine Lake resident, pers. comm.). Unlike Interior Alaska, extremely cold winter temperatures (<-17°C) are rare although ice forms on the rivers in October with breakup in late May. During 1988, summer water temperatures approached 19°C during August with an estimated average of approximately 1500 degree days (above 0°C) accumulated for the study streams (Figure 3.2).

All watersheds are free from major anthropogenic disturbance. The vegetation is largely birch (*Betula papyrifera*), poplar (*Populus tacamahacca*) and white spruce (*Picea glauca*). Thick willow (*Salix* spp.) and alder (*Alnus* spp.) stands dominate riparian zones.

The highest peaks of the western Talkeetna Mountains are ≤2000 m. Tree-line averages ≈800 m. Watershed areas of study streams range from 54 km^2 to 336 km^2. Stream gradients averaged from 7 $m \cdot km^{-1}$ to 37 $m \cdot km^{-1}$ for the 3 km above each study site, while elevations of the sampling-site location ranged from 182 m to 655 m. Byers Creek, Pass Creek and Troublesome Creek had substantial ponds and lakes in their upper reaches.

FIGURE 3.2. Water temperatures of study streams during 1988. Temperature at each date respresents the average of the high and low values recorded (with high-low thermometer) for the ~~two~~ 2 weeks prior to that date at the specific site.

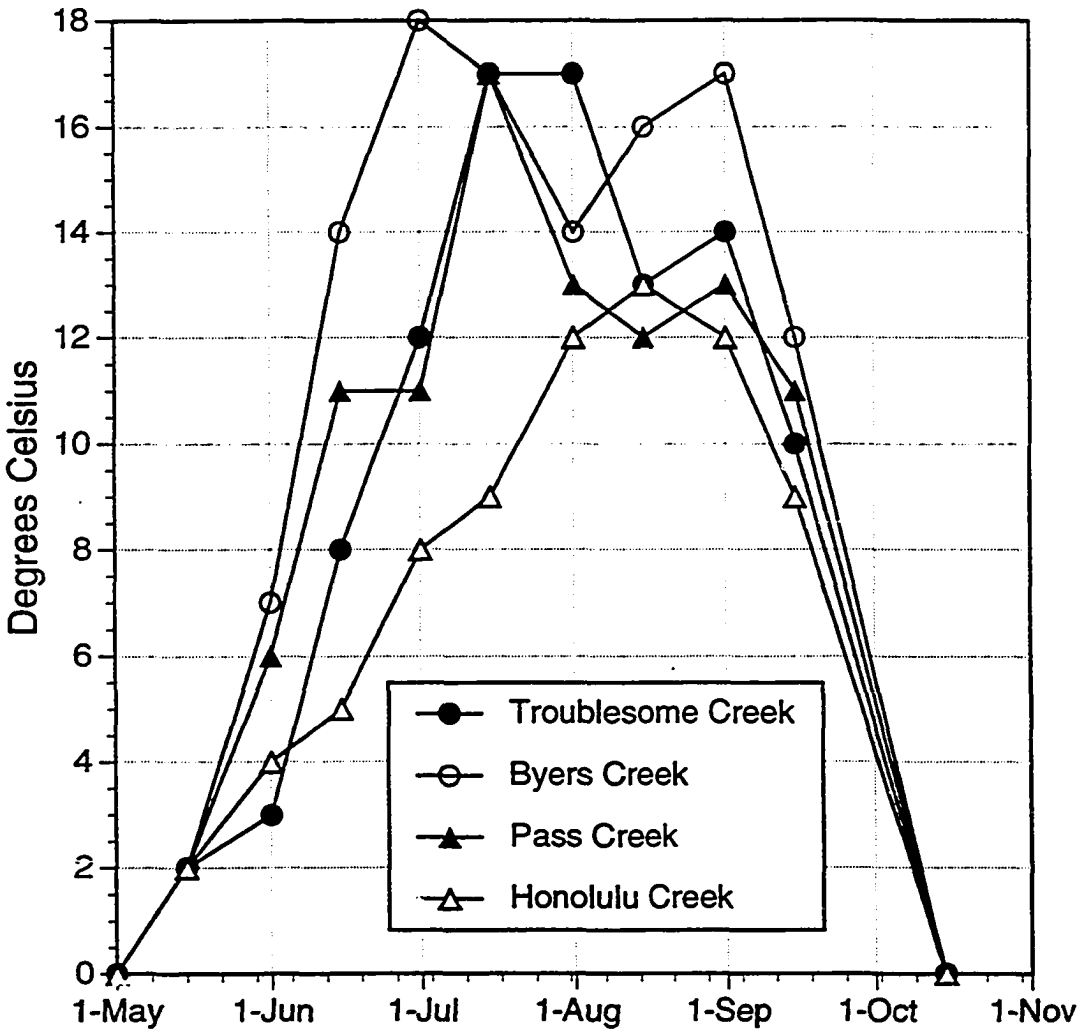


TABLE 3.1. Physical characteristics of study streams. Stream order based on USGS maps with 1:63,360 scale. Stream discharge represents summer baseflow.

Stream	Stream Order (Strahler)	Sample site elevation (m)	Water-shed area (km^2)	Lakes/ ponds (km^2)	Stream gradient ($m \cdot km^{-1}$)	Stream discharge ($m^3 \cdot sec^{-1}$)
Byers Creek	3	335	91	≈7.8	9	4.1
East Fork Chulitna River	4	541	336	none	12	16.0
Honolulu Creek	3	457	168	none	12	7.0
Middle Fork Chulitna River	3	655	114	none	14	7.3
Lower Pass Creek	3	335	54	downstream from U. P. inputs	18	2.4
Upper Pass Creek	3	381	54	≈1.5	7	1.8
Lower Troublesome Creek	3	182	98	downstream from U. T. inputs	28	2.5
Upper Troublesome Creek	3	335	98	≈2.0	37	2.3

TABLE 3.2. Substrate composition of study streams at sampling locations. All measurements in %.

	Substrate diameter and percent composition in streambed						
	Silt	Sand	1-7 cm	7-15 cm	15-25 cm	>25 cm	Embedded -ness
Byers Creek	0	10	10	10	30	40	25
East Fork Chulitna River	0	10	10	20	40	20	25
Honolulu Creek	0	10	10	20	30	30	25
Middle Fork Chulitna River	0	10	20	50	10	10	25
Lower Pass Creek	10	10	30	30	10	10	50
Upper Pass Creek	10	10	30	30	10	10	50
Lower Troublesome Creek	0	10	10	20	30	30	25
Upper Troublesome Creek	0	10	10	10	30	40	<25

Typical baseflow discharge during July, August, and September 1993 ranged from ≈1.8 $m^3 \cdot sec$ to ≈16 $m^3 \cdot sec^{-1}$ (Table 3.1). Small to large cobble are the predominant stream substrate (Table 3.2) with glacial till being the prevalent soil type throughout the watersheds (Tom Bundzen, Geological Survey, State of Alaska, pers. comm.). Streambed movement was noted at all sites during seasonally common flood. Two streams, Pass Creek and Troublesome Creek have waterfalls of sufficient height (>5 m) to prevent salmon movement beyond those points.

During 1989, chemical measurements of study streams showed them to be comparable. Alkalinity was low, ranging from 17 to 34 mg l^{-1} as $CaCO_3$. Conductance fluctuated from 14 micromhos/cm to 40 micromhos/cm. The pH was low during winter break-up (pH≈5) and high-water events, but otherwise was near neutrality. During July, August, and September 1993, major nutrient concentrations in waters of study stream were measured. Total dissolved phosphorus (TDP) ranged from undetectable to 13 µg l^{-1} whereas total dissolved nitrogen (TDN) ranged from 0.04 mg l^{-1} to 0.54 mg l^{-1} (Table 3.3).

Dependable historic data on strength of salmon runs in Upper Chulitna River drainages was unavailable, but all study streams possessed salmon runs of different magnitude. Thick riparian-zone vegetation, high stream gradients, and vast watersheds make all streams difficult to survey on foot, with questionable accuracy even under optimum conditions. Low water in 1988 allowed for an approximate estimate of typical run strength. Continual high waters in 1989 and 1990 made similar estimates impossible. Byers Creek has the largest runs, with all five species of pacific salmon; ≈1000 king, ≈2000 red, ≈1000 silver, ≈1000 dog and ≈3000 pink. Both Lower

TABLE 3.3. Water chemistry measurements from study streams. Total dissolved nitrogen and total dissolved phosphorus values represent an average of 3 measurements taken during July, August and September of 1993. All other values represent an average of 4 measurements taken during May, June, August and September of 1989. The range of values is in parentheses.

	pH	Alkalinity mg l^{-1} $CaCO_3$	Conductance µmhos cm^{-1}	TDN mg l^{-1}	TDP µg l^{-1}
Byers Creek	6.0 (4.8-7.2)	29.8	26.5	0.44 (0.36-0.41)	4 (2-6)
East Fork Chulitna River	---	---	---	0.10 (0.06-0.18)	4 (1-10)
Honolulu Creek	5.8 (4.8-7.0)	29.8 (17-34)	34 (30-40)	0.11 (0.05-0.15)	2 (0-5)
Middle Fork Chulitna River	---	---	---	0.06 (0.04-0.07	1 (0-2)
Lower Pass Creek	5.6 (4.9-6.8)	32.5 (28-34)	23.5 (18-31)	0.34 (0.32-0.38)	7 (4-10)
Upper Pass Creek	5.5 (5.2-6.5)	34 (34)	23.3 (19-30)	0.25 (0.18-0.32)	7 (6-10)
Lower Troublesome Creek	5.9 (4.5-7.1)	29.8 (17-34)	20 (17-26)	0.40 (0.31-0.55)	7 (4-13)
Upper Troublesome Creek	6.0 (4.8-6.9)	26 (17-34)	15 (12-18)	0.31 (0.26-0.34)	5 (2-8)

Troublesome and Lower Pass Creeks have similar runs (≈1000) of king salmon, but there are no red salmon in either creek. While Troublesome Creek receives runs of the other species of salmon comparable to Byers Creek, Pass Creek receives ≈1/10 the salmon. Small runs of king salmon were seen in the Middle Fork Chulitna River (≈150), the East Fork Chulitna River (≈50) and Honolulu Creek (≈20). No salmon occur in Upper Troublesome Creek and Upper Pass Creek due to impassable waterfalls.

For statistical analysis, I ranked the streams (See Table 3.4) from most enriched to least enriched by two parameters; 1) average strength of salmon escapement to the system; and 2) area of ponds and lakes upstream (Table 3.1). Systems with no enrichment were given a tied rank at one rank below the last rank that had enrichment.

The yearly cycle of the salmon runs start with king salmon entering streams by the middle of June. Peak spawning activity occurs from late June through early July with most fish dead and decomposed by the end of July. Dog salmon and pink salmon enter the creeks during early August, spawning and dying by that month's end. Silver salmon spawn from mid-August through mid-September with rare individuals still alive and spawning in early October (Figure 3.3).

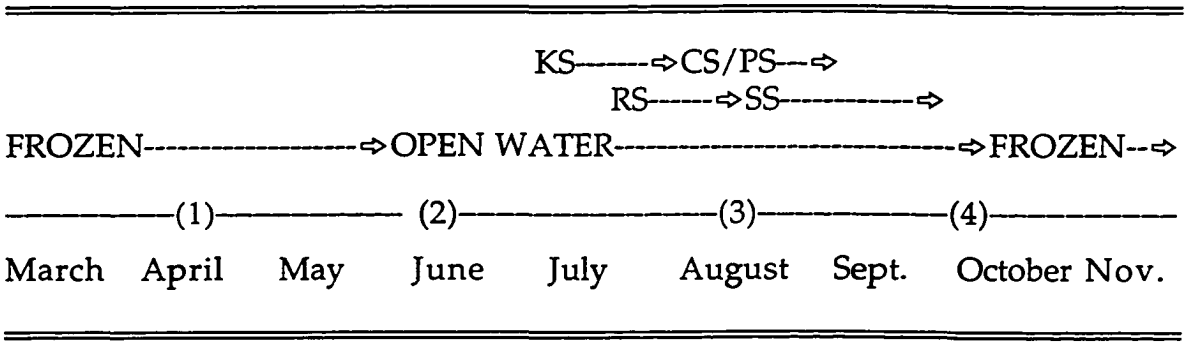
Site descriptor protocol

One sampling site was established on each of the six aforementioned study streams. Another sampling site was established on Pass Creek 3 km downstream from the highway below a 30 m waterfall. An eighth sampling site was located 10 km upstream from the highway above a 5 m waterfall on Troublesome Creek. General water chemistry measurements were taken

Table 3.4. Study streams ranked in potential for macroinvertebrate community enrichment from either salmon carcasses or discharge from lakes and ponds. Lowest number has the highest potential for enrichment. Regression analysis used this ranking as the independent variable. The overall potential for enrichment comes from the sum of these two ranks.

Enrichment potential from salmon carcasses	
1	Byers Creek
2	Lower Troublesome Creek
3	Lower Pass Creek
4	Middle Fork Chulitna River
5	East Fork Chulitna River
6	Honolulu Creek
7	Upper Pass Creek
7	Upper Troublesome Creek
Enrichment potential from ponds and lakes	
1	Byers Creek
2	Upper Troublesome Creek
3	Upper Pass Creek
4	Lower Troublesome Creek
5	Lower Pass Creek
6	East Fork Chulitna River
6	Honolulu Creek
6	Middle Fork Chulitna River
Combined enrichment potential	
1	Byers Creek
2	Lower Troublesome Creek
3	Lower Pass Creek
4	Upper Troublesome Creek
5	Middle Fork Chulitna River
5	Upper Pass Creek
6	East Fork Chulitna River
7	Honolulu Creek

Figure 3.3. Monthly phenology of sampling protocol in relationship to salmon-spawning activities and stream ice cover. Upper case letters indicate spawning period for each salmon species using creek (KS=king salmon, RS=red salmon, CS=chum salmon, PS=pink salmon, and SS=silver salmon). Stream ice-free period delineated. Numbers in parentheses indicate sampling period.



during ecologically distinct time periods. These times were pre-breakup, while the streams were mostly frozen (late April), post break-up and pre-salmon (mid-June), middle of salmon runs (mid-August) and post-salmon runs (early October) (Figure 3.3). All samples for each time period were collected during two days of stable weather to limit stormflow-induced variations on chemical measurements.

Water temperatures were recorded every two weeks from May through October 1988 with a high-low, manual re-set thermometer (Taylor Instruments, Fletcher, North Carolina). Thermometers were in perforated, 1-m long sections of 10-cm ABS sewer pipe manually imbedded 0.5-m vertically into the stream substrate. Tops of these pipes remained submerged despite fluctuating water levels. The upright stance of the pipes allowed easy positioning and retrieval of thermometers. Water temperatures within and outside the perforated pipes were always the same. Temperatures were recorded and high-low devices reset every 2 weeks throughout this sampling period. Watershed area, stream gradients, and sampling site elevations were determined from United States Geological Surveys maps (1:63,360). Stream substrate composition was visually estimated.

Stream current was measured using a Direct Reading Current Meter by Teledyne Gurley (Troy, New York). Except for the East Fork Chulitna River, which was too fast and deep, a section of each stream was selected for discharge determination that was wadable, possessed a relatively smooth bottom and contained the entire flow of the stream. A 30-m measuring tape was stretched across watercourse and secured at both ends. Measurements of depth and velocity at 0.4 of depth as measured upwards from the streambed at

1-m intervals along the tape measure were recorded. Approximate stream discharge was calculated from these measurements. The East Fork Chulitna River width was estimated. Current and depth was measured for 5-m from each bank and estimated for the deep or swift parts of the river.

During 1989, study stream water chemistry measurements were taken. Three samples of water were taken at 0.1 stream depth from midstream at each site at each date. Measurements did not vary among replicates. Acidity was determined with pH Indicator Strips (EM Science, Gibbstown, N.J.). A Hach Portable Conductivity Meter (catalog #46414) was used to measure conductivity. A Hach kit utilizing colorimetric titration to an indicator endpoint was used to measure alkalinity.

Water samples for measurement of total nitrogen (TN) and total phosphorus (TP) were collected in 1993 during July, August, and September. These dates were chosen because effects of salmon runs on stream nutrient levels would be maximized. Water samples were collected in 125 ml acid-rinsed polybottles from mid-stream just below the surface. Bottles and caps were rinsed with stream water three times before the sample was taken. Once the sample was collected and the lid was secured tightly, the bottle was immediately placed in crushed ice and was frozen within 24 hours. Analyses of samples for TN (Crumpton et al. 1992) and TP (American Public Health Association 1985) were carried out in the Laboratory of . J. R. Jones, Department of Fisheries and Wildlife, University of Missouri-Columbia.

Macroinvertebrate collection and analysis

To encompass seasonal variation in life history patterns, samples of benthic macroinvertebrates were collected during 4 ecologically different periods in both 1988 and 1990. These times were pre-breakup, when the

streams were mostly frozen (late April), post break-up and pre-salmon run (mid-June), middle of salmon runs (mid-August) and post salmon runs (early October) (Figure 3.3). Given mercurial weather conditions, all samples for each period were collected during 2 days of stable weather to limit storm-induced changes in communities of benthic macroinvertebrates.

Macroinvertebrate samples were collected in 1988 and 1990 using a rectangular (460 mm x 200 mm) 'Bottom Aquatic Kick Net' (mesh: 800 μm x 900 μm) from WildCo Supply Co., Saginaw, Michigan. Each sample site was approximately 50-m long and stream-width wide, encompassing representative microhabitats (runs, riffles, pools, and large woody debris). While holding the net downstream from myself, I kicked and scraped all substrate to a depth of ≈10 cm while moving down the length of each study stretch. This was repeated along lines parallel to the first collecting course. This sampling technique provided semi-quantitative data (information on relative, but not absolute, abundance of benthic invertebrate taxa). Semi-quantitative sampling of the entirety of large reaches containing representative microhabitats had two advantages: (1) sampling of such a very large area provided the large biomass necessary for the stable-isotope analysis, separately published, part of this study; and, (2) conventional quantitative samplers (e.g., Surber sampler) would have been unusable in deep water and on large substrate. In 1988, approximately 0.5 hour was spent collecting each sample. After analysis of 1988 data showed size of samples insufficient for stable-isotope analysis, approximately 1 hour was spent collecting each sample in 1990.

Benthic material collected at each site was first washed into the bottom

of the collecting net to form a bolus. This bolus was then placed into a 1000 ml wide-mouth polybottle. Labels identifying location, date and collector were placed on the inside and outside of the bottle. The sample was then immersed in crushed ice until frozen. Late instar macroinvertebrates destined for stomach analysis were hand-picked from rocks and debris with forceps and placed in labeled vials filled with 80% ETOH.

In the laboratory, benthic samples were thawed. Macroinvertebrates were removed from associated detritus using a WILD [Model Five] dissecting microscope. After sorting, the numbers of individuals in each taxon were counted. Individuals from each separate taxon were then air-dried enmasse. After drying, the weight of each taxon (in milligrams) was recorded. All macroinvertebrates from 1988 were classified at least to family while 1990 macroinvertebrates were taken to genus (except Chironomidae and Ceratapogonidae) using Merritt and Cummins (1978), Pennak (1978), Stewart and Stark (1988) and Wiggins (1977). Taxa were placed into one of the following functional feeding groups; collector-gatherer, filterer, predator, scraper and shredder (Merritt and Cummins (1978); and Hawkins and Sedell (1981)) (Table 3.5). These classifications were confirmed through limited gut analysis using a protocol described by Cowan et al. (1983) (Table 3.6). Chironomidae guts were not examined due to both their extremely small individual size, making such analysis difficult, and the group's comparatively small overall contribution to community biomass. Past research in interior Alaska streams indicates that the dipteran family Chironomidae predominantly functions as collector-gatherers (Steven Peek, Institute of Arctic Biology, University of Alaska, Fairbanks, pers. comm.).

TABLE 3.5. Lotic macroinvertebrate taxa occurring in study streams in Denali State Park and vicinity, Alaska. Their functional feeding group was obtained from Merrit and Cummins (1978).

Annelida	Oligochaeta	Lumbriculidae	*Rhynchelmis*	collector-gatherer
Arachnoidea	Hydracarina	Hydrodromidae	*Hydrodroma*	predator
Insecta	Diptera	Ceratapogonidae		predator
		Chironomidae		collector-gatherer
		Empididae	*Chelifera*	predator
			Clinocera	predator
		Psychodidae	*Pericoma*	collector-gatherer
		Simuliidae	*Prosimulium*	filterer
			Simulium	filterer
		Tipulidae	*Dicranota*	predator
			Tipula	shredder
	Ephemeroptera	Baetidae	*Baetis*	collector-gatherer
		Ephemerellidae	*Drunella*	predator
			Ephemerella	collector-gatherer
		Heptageniidae	*Cinygmula*	scraper
			Epeorus	collector-gatherer
			Heptagenia	scraper
			Ironodes	scraper
			Rithrogena	collector-gatherer
		Siphlonuridae	*Ameletus*	collector-gatherer
	Plecoptera	Capniidae	*Allocapnia*	shredder
			Paracapnia	shredder
		Chloroperlidae	*Neaviperla*	predator
			Plumiperla	predator
		Nemouridae	*Malenka*	shredder
			Nemoura	shredder
			Soyedina	shredder
			Zapada	shredder
		Perlodidae	*Arcynopteryx*	predator
			Isoperla	predator
		Pteronarcidae	*Pteronarcella*	shredder
		Taeniopterigidae	*Doddsia*	shredder
	Trichoptera	Brachycentridae	*Amiocentris*	collector-gatherer
			Brachycentrus	filterer
		Glossosomatidae	*Glossosoma*	scraper
		Hydropsychidae	*Arctopsyche*	filterer
			Hydropsyche	filterer
		Hydroptilidae	*Oxyethira*	scraper
		Limnephilidae	*Amphicosmoecus*	shredder
			Apatania	scraper
			Chyranda	shredder
			Desmona	shredder
			Eclisocosmoecus	shredder
			Ecclisomyia	shredder
			Grensia	shredder
			Hydatophylax	shredder
			Limnephilius	shredder
			Onocosmoecus	shredder
			Psychoglypha	collector-gatherer
		Rhyacophilidae	*Rhyacophila*	predator
Mollusca	Gastropoda	Lymnaeidae	*Lymnaea atkaensis*	scraper
		Planorbidae	*Helisoma trivolis*	scraper
	Pelecypoda	Sphaeridae	*Sphaerium nitidum*	filterer
Nematoda	?			collector-gatherer
Turbellaria	Tricladida			collector-gatherer

TABLE 3.6. Gut contents of predominant insect taxa occurring in study streams in Denali State Park and vicinity, Alaska. n=number of individual guts examined, numbers are relatively proportion of specific food type observed, and tr=trace of food type observed.

Taxon	Gut Contents			
	Plant detritus	Diatoms	Animal	Unrec. detritus
Diptera				
Tipulidae				
Dicranota (n=12)	tr		40	60
Tipula (n=2)	40		40	20
Ephemeroptera				
Ephemerellidae				
Drunella (n=15)	tr	60	40	tr
Ephemerella (n=17)	tr	20	60	20
Heptageniidae				
Heptagenia (n=4)	20	80	tr	tr
Ironodes (n=3)		100		
Rithrogena (n=4)	20	40	20	20
Siphlonuridae				
Ameletus (n=5)	20	20	40	20
Plecoptera				
Chloroperlidae				
Plumiperla (n=9)			100	tr
Perlodidae				
Arcynopteryx (n=9)			100	
Isoperla (n=12)			100	tr
Taeniopterigidae				
Doddsia (n=3)	80			20
Trichoptera				
Brachycentridae				
Brachycentrus (n=11)	20	tr	80	tr
Hydropsychidae				
Arctopsyche (n=8)	tr	tr	100	tr
Limnephilidae				
Ecclisomyia (n=13)	80	tr	20	
Hydatophylax (n=6)	20	20	60	tr
Onocosmoecus (n=8)	100	tr	tr	
Psychoglypha (n=7)	20		40	40

Statistical analysis

Because many ecologists agree that the importance of any part (e.g., taxon or functional group) of a community should be based on biomass (Hurlburt 1971, Lyons 1981), the biomass of each group, rather than the number of individuals within the group, was used in statistical analyses. The weight of each group in each sample was transformed into percent of the total dry weight of the macroinvertebrate community for each sample. The average dry weight of an individual in a taxon at a particular time was calculated by dividing the dry weight of the entire taxon at a particular time by the number of individuals in it.

These relative abundance values were used to calculate estimates of evenness (Hill's ratio) and diversity (Hill's numbers) for each sample (Hill 1973) whereas direct counts of taxa were used to compare richness between streams. Hill's ratio was chosen because it is maximum when the taxa are evenly distributed, is considered the least ambiguous of the evenness indices and does not require an estimate of the number of taxa in a community (Ludwig and Reynolds 1988). Diversity indices are combinations of taxa richness and evenness indices, thus differing values of components may result in the same end value making interpretation difficult. Hill's numbers, unique in only using proportional data (numbers or weight of individuals in a group and total number or total weight of individuals), are proclaimed by Peet (1974) as suitable for "addressing any question a heterogeneity index can answer." Direct counts of taxa were chosen as a richness indicator as sample sizes were approximately equal and, unlike other indices, they do not require a functional and constant relationship between the number of taxa and number of individuals collected (Ludwig and Reynolds 1988).

Data were analyzed with simple linear regression. Considered robust enough for nonnormal distributions (Zar 1974), regression analyses were done using the statistical program STATVIEW©, (Abacus Concepts, Berkeley, California). Test results (p values) are reported in the following manner; between 0.10 and 0.05 as marginally significant, between 0.05 and 0.01 as significant, and < 0.01 as highly significant. Statistical analyses (regression) were not corrected for experiment-wide error rate; exploratory data analysis was of greater importance than maintaining tight control of type I error across all analyses.

RESULTS

Macroinvertebrate collections

Ten orders, five functional groups, and 54 taxa (mostly genera) were present among the 122,138 macroinvertebrates collected during 1988 and 1990 (APPENDIX A). Increased collection effort per sample in 1990 and the two additional study sites caused both the average number of macroinvertebrates collected per sample and their dry biomass to more than double when compared to 1988 samples. The average dry weight per individual macroinvertebrate per sampling period decreased in 1990 (Table 3.7). This probably is the result of the addition in 1990 of two previously unsampled streams, (with smaller individuals), rather than the targeting of macroinvertebrates of smaller size.

Richness, evenness and diversity

Regression analysis of aforementioned indices (1988 and 1990 data analyzed separately) as a function of degree of enrichment by salmon carcasses (SM), lake outlet effect (LK) and combination of both effects (BT) resulted in several statistically significant values (Table 3.8 and Figure 3.4). Richness indices showed a marginally significant increase for BT in 1988 and SM in

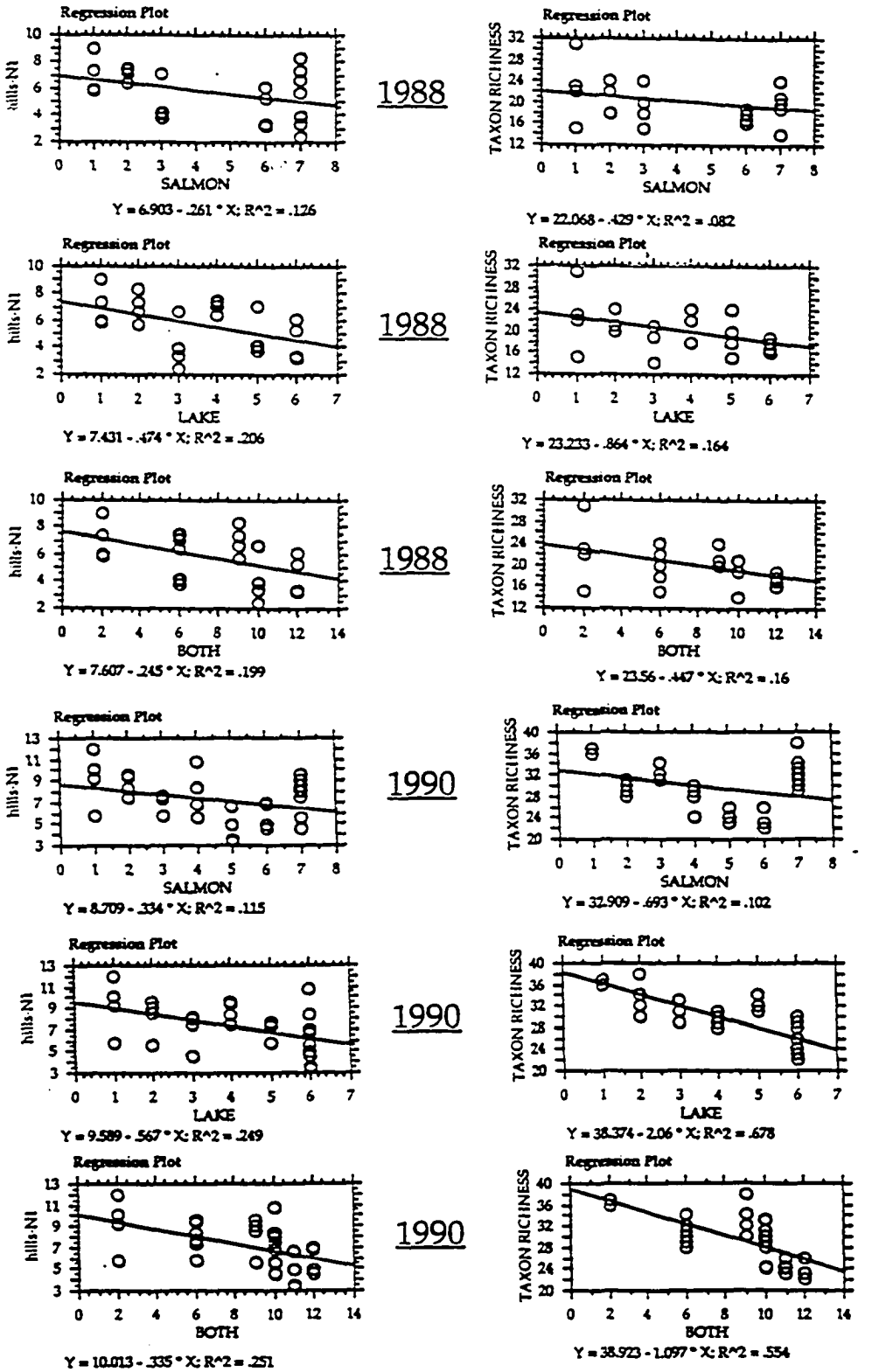
TABLE 3.7. Average macroinvertebrate numbers and dry weights for benthic samples collected at four sample sites on Troublesome and Pass Creeks (Alaska) in 1988 and 1990. (mean ±1 SE: n=number of samples)

Variable	1988 (n=24)	1990 (n=32)
Total macroinvertebrates collected	27,758	94,372
Average number of individual macroinvertebrates per sample	1157±177 (range: 175 to 3653)	2949±209 (range: 726 to 5442)
Total macroinvertebrate dry biomass collected	11,991 mg	45,764 mg
Average dry macroinvertebrate biomass per sample	499±48 mg (range: 105 to 1127)	1430±144 mg (range: 234 to 3732)
Average dry weight per individual macroinvertebrate per sample	0.76±0.22 mg. (range: 0.06 to 2.76)	0.52±0.12 mg. (range: 0.09 to 0.81)

TABLE 3.8. Results of regression analyses (P values) of ranked enrichment (salmon, lake, combination of both) versus calculated richness, evenness and diversity values for the macroinvertebrate community in study streams.

	Richness		Evenness		Diversity	
	1988	1990	1988	1990	1988	1990
Salmon	n.s.	0.07	n.s.	n.s.	0.05	0.05
Lake	n.s.	0.001	n.s.	n.s.	0.02	0.008
Salmon+Lake	0.07	0.001	n.s.	n.s.	0.03	0.003

FIGURE 3.4. Regression plots for macroinvertebrate richness and diversity indices for 1988 and 1990 versus degree of enrichment. Enrichment calculated from from Table 3.4.



1990. There was a highly significant increase for LK and BT in 1990. Evenness indices (Hills ratio) showed no relationship to enrichment for either year. Diversity indices (Hill's numbers) showed marginal to highly significant increases for both years for SM, LK and BT.

Diptera/Ephemeroptera/Plecoptera/Trichoptera/non-insects

Taxa from the order Ephemeroptera comprised proportionally the most biomass in the study streams, followed closely by taxa in the order Trichoptera. Members of the orders Plecoptera and Diptera generally composed a smaller portion of total biomass whereas noninsects were the smallest portion (Table 3.9). Measurements diptera biomass should be viewed with caution: they may be low due to probable loss of early instars through the relatively large mesh of the collecting net. Regression analyses of proportional representation of these groups against degree of enrichment for 1988 resulted in Plecoptera biomass being negatively associated with LK, while Trichoptera biomass was positively associated with this same variable. In 1990, these relationships continued, with both also having highly significant values for BT. Also in 1990, Diptera and Ephemeroptera biomass were negatively associated with both LK and a BT (Table 3.10).

Taxa, functional groups, sample biomass and individual weights

Individual macroinvertebrate weight per sample and absolute sample biomass were regressed against the degree of enrichment for 1988 and 1990 (Figure 3.5). Individual weight was significantly associated (positively) with salmon and a combination of both effects in 1990. Regression of both enrichment effects showed them to be additive for both years (Figure 3.5).

Regression analyses of taxon and functional group specific individual

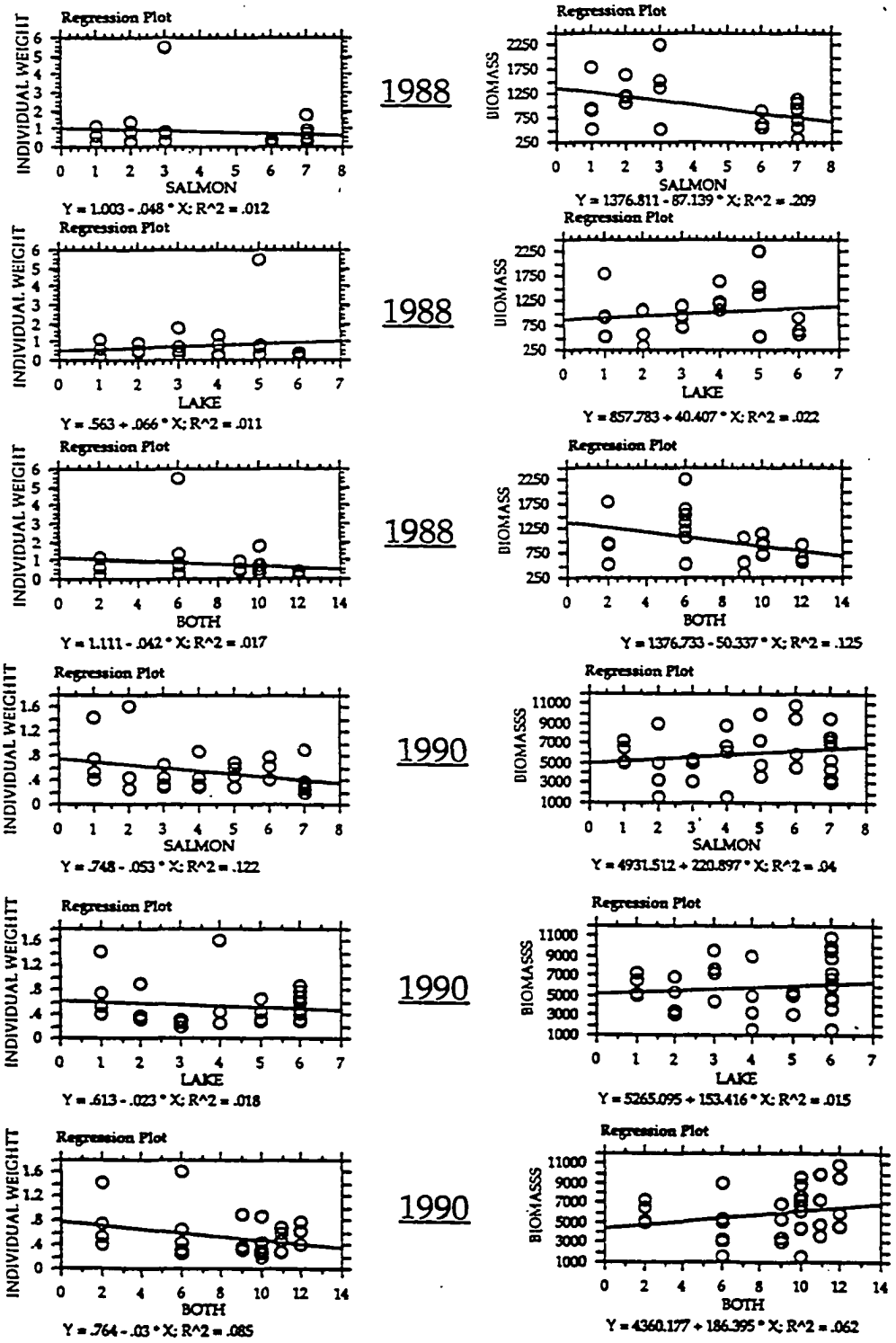
TABLE 3.9. Proportional biomass of Diptera, Ephemeroptera, Plecoptera, Trichoptera and noninsects (%) from study streams in Denali State Park and vicinity, Alaska during 1988 and 1990. (mean ±1 SE: n=number of samples)

Taxa	1988 (n = 24)	1990 (n = 32)
Diptera	8.1±1.1 (range: 0.4 to 27)	6.8±0.9 (range: 0.9 to 20.9)
Ephemeroptera	47.3±4.8 (range: 7.3 to 89.7)	51.5±4.4 (range: 5.7 to 89.1)
Plecoptera	5.8±1.3 (range: 0.2 to 22.9)	13.3±2.1 (range: 1.1 to 49.8)
Trichoptera	37.6±4.9 (range: 6.2 to 83.4)	27.2±3.7 (range: 0.1 to 88.0)
Noninsects	1.0±0.3 (range: 0.0 to 5.9)	1.3±0.3 (range: 0.03 to 8.31)

Table 3.10. Relationships between proportional biomass of certain macroinvertebrate orders common to study streams and the degree of enrichment that streams receive. Type of enrichment; S=salmon, L=lake, B=combination of both. No significant difference due to enrichment indicated by (·). Plus (+) or minus (-) signs indicates direction of response to enrichment. ms=marginally significant (0.05<P<0.10), s=significant (0.01<P<0.05), hs=highly significant (P<0.01).

Date	Diptera			Ephemeroptera			Plecoptera			Trichoptera		
	S	L	B	S	L	B	S	L	B	S	L	B
1988-April	·	·	·	·	·	·	·	·	·	·	·	·
June	·	·	·	·	·	·	·	-ms	·	·	·	·
August	·	-s	·	·	-ms	·	·	·	·	·	·	·
October	·	·	·	·	·	·	·	·	·	·	·	·
1988-Ave.	·	·	·	·	·	·	·	-s	·	·	+s	·
1990-April	·	·	·	·	-ms	·	·	-ms	-s	·	+hs	·
June	·	·	·	·	-ms	·	·	·	·	·	+hs	·
August	·	·	·	·	-hs	-hs	·	·	·	·	+hs	+hs
October	·	-hs	-s	·	-s	·	·	·	·	·	+s	·
1990 Ave.	·	·	-ms	·	-hs	-s	·	-s	-s	·	+hs	+s

FIGURE 3.5. Regression plots for sample biomass and individual weight for versus degree of enrichment 1988 and 1990. Enrichment calculated from Table 3.4.



macroinvertebrate weight and proportional biomass versus degree of enrichment were performed for the eight sampling periods in 1988 and 1990 (Table 3.11). Of the taxa and functional groups in all or most systems, an average of 38% of 26 per sampling period showed at least a marginally significant enrichment effect in 1988 and an average of 60% of 43 per sampling period showed at least a marginally significant enrichment effect in 1990. This increase may stem from the more refined classification of taxa and the larger sample size in 1990. Twenty taxa were not included in regression analyses because they were either rare or were restricted to salmon and lake systems (Table 3.12). The combined total number of marginally significant or greater test results for both sampling years was largest for a combination of BT (149), next for LK (119) and least for S (79).

All relationships described in the following discussion of Table 3.11 were at least marginally significant. During 1988, collector-gatherers, filterers and predators often were larger individually in enriched systems. Chironomidae were smaller in enriched systems in June and larger in enriched systems in August. *Drunella* was consistently larger individually and in proportional biomass in enriched systems in April, but smaller in both parameters by June. *Brachycentrus* displayed a significant enrichment effect in biomass during June. *Arctopsyche*, was the only taxon to consistently show an enrichment effect (positive) across all four sampling periods.

In 1990, filterers and collector-gatherers generally showed an increase in individual size and proportional biomass with enrichment, while predators, scraper-grazers and shredders responded negatively to enrichment in spring and positively in Autumn. Chironomidae were generally smaller

TABLE 3.11. Results of regression analyses placing individual macroinvertebrate weight and proportional biomass for each taxon and functional group against degree of enrichment for eight sampling periods in 1988 and 1990. MS=marginally significant (0.05<P<0.10), S=significant (0.01<P<0.05) and HS=highly significant (P<0.01). Plus (+) or minus (-) indicates direction of response to enrichment.

1988-APRIL SAMPLES		REGRESSION					
FUNCTIONAL GROUP/TAXON		SALMON		LAKE		COMBINED	
	±	I.W.	%WT	I.W.	%WT	I.W.	%WT
-COLLECTOR/GATHERER-	+	S	S-	.	.	S	MS
-PREDATOR-	+	.	MS	.	.	.	.
DIPTERA: Prosimulium	+	.	MS	.	.	.	S
EPHEMEROPTERA: Heptagenidae	+	MS	.	.	.	.	.
Drunella	+	S	S	.	.	.	MS
Ephemerella	+	S	.	.	.	S	.
PLECOPTERA: Zapada	-	.	.	.	.	.	MS
Isoperla	-	.	.	S	S	.	MS
TRICHOPTERA: Arctopsyche	+	.	.	.	.	S	S

1988-JUNE SAMPLES		REGRESSION					
FUNCTIONAL GROUP/TAXON		SALMON		LAKE		COMBINED	
	±	I.W.	%WT	I.W.	%WT	I.W.	%WT
-PREDATOR-	+	S	.	.	.	S	.
DIPTERA: Chironomidae	-	MS	.	.	.	.	MS
EPHEMEROPTERA: Heptagenidae	-	.	.	.	.	.	MS
Drunella	-	MS	.	.	.	.	.
Ameletus	-	.	.	.	.	MS	MS
TRICHOPTERA: Brachycentrus	+	.	.	.	S	.	S
Glossosoma	-	.	.	.	.	.	MS
Arctopsyche	+	.	.	.	.	MS	MS
Psychoglypha	+	.	.	MS	S	MS	.
TURBELLARIA	+	.	.	.	.	MS	MS

1988-AUGUST SAMPLES		REGRESSION					
FUNCTIONAL GROUP/TAXON		SALMON		LAKE		COMBINED	
	±	I.W.	%WT	I.W.	%WT	I.W.	%WT
-COLLECTOR/GATHERER-	+	S	.	.	.	MS	.
-FILTERER-	+	.	S	.	S	.	MS
HYDRACARINA	-	.	.	MS	.	.	.
DIPTERA: Ceratopogonidae	+	.	S	.	S	.	MS
Chironomidae	+	.	.	MS	.	.	.
Empididae	+	.	S	.	.	.	S
Tipula	+	.	.	.	.	.	MS
PLECOPTERA: Isoperla	+	.	.	.	.	MS	.
TRICHOPTERA: Brachycentrus	+	MS	.	.	.	.	.
Glossosoma	+	.	MS	.	.	.	.
Arctopsyche	+	.	.	.	.	.	MS
Hydropsyche	+	.	.	.	S	.	.
Psychoglypha	+	.	.	S	.	MS	.

1988-OCTOBER SAMPLES		REGRESSION					
FUNCTIONAL GROUP/TAXON		SALMON		LAKE		COMBINED	
	±	I.W.	%WT	I.W.	%WT	I.W.	%WT
-FILTERER-	+	.	.	S	.	MS	.
-SHREDDER-	-	.	.	.	MS	.	.
OLIGOCHAETA	+	.	.	.	.	MS	MS
DIPTERA: Pericoma	+	.	.	.	.	MS	MS
Tipula	+	.	.	.	.	MS	.
EPHEMEROPTERA: Baetis	+	.	.	.	.	MS	MS
PLECOPTERA: Plumiperla	-	.	.	.	S	.	S
Isoperla	+	.	.	.	.	MS	MS
TRICHOPTERA: Arctopsyche	+	.	.	MS	S	.	S

1990-APRIL SAMPLES		REGRESSION					
FUNCTIONAL GROUP/TAXON		SALMON		LAKE		COMBINED	
	±	I.W.	%WT	I.W.	%WT	I.W.	%WT
-FILTERER-	+	S	.	HS	HS	HS	S
-PREDATOR-	-	S	.	.	.	.	.
-SCRAPER/GRAZER-	-	.	S	.	MS	.	S
-SHREDDER-	-	MS	.	S	.	.	MS
DIPTERA: Chironomidae	-	.	.	S	.	.	.
Pericoma	+	S	S	.	.	S	MS
Dicranota	+	MS	.	.	.	S	.
EPHEMEROPTERA: Drunella	-	.	.	.	S	.	.
Ironodes	-	.	MS	.	MS	.	S
Rithrogena	+	.	S	.	MS	.	S
Ameletus	-	.	HS	.	.	.	S
PLECOPTERA: Plumiperla	+	MS	.	.	.	.	MS
Zapada	±	MS+	.	S-	.	.	.
Isoperla	-	S	.	.	.	S	.
Doddsia	-	.	S	.	MS	.	S
TRICHOPTERA:Brachycentrus	+	S	.	S	S	HS	.
Arctopsyche	+	MS	.	S	S	S	S
Hydropsyche	+	.	.	.	MS	.	MS
Onocosmoecus	+	.	MS	.	.	S	.
Rhyacophila	+	HS	.	.	.	HS	.

1990-JUNE SAMPLES		REGRESSION					
FUNCTIONAL GROUP/TAXON		SALMON		LAKE		COMBINED	
	±	I.W.	%WT	I.W.	%WT	I.W.	%WT
-COLLECTOR/GATHERER-	+	S	.	.	.	MS	MS
-FILTERER-	+	MS	.	HS	S	HS	.
-SCRAPER/GRAZER-	-	.	.	MS	.	.	.
DIPTERA: Chironomidae	-	MS	MS	.	.	MS	MS
Chelifera	+	.	.	.	.	MS	.
Tipula	-	.	.	MS	.	S	.
EPHEMEROPTERA: Baetis	-	.	.	S	MS	S	MS
Drunella	+	.	MS	.	.	.	.
Ephemerella	+	MS	.	.	HS	.	MS
Cinygmula	+	S	.	MS	.	S	.
Heptagenia	+	.	.	HS	.	S	.
Ironodes	-	.	.	MS	.	.	.
Rithrogena	+	.	.	.	S	.	.
Ameletus	+	.	MS	.	.	.	.
TRICHOPTERA: Amiocentris	+	.	.	MS	MS	MS	MS
Brachycentrus	+	.	.	S	S	S	.
Arctopsyche	+	.	.	S	.	S	.
Hydropsyche	+	.	MS	MS	MS	.	S
Apatania	+	.	.	.	.	.	MS
Ecclisomyia	+	MS	S	MS	S	S	S
Onocosmoecus	+	.	MS	.	MS	.	S
GASTROPODA	+	.	.	.	.	MS	S
TURBELLARIA	+	.	.	MS	MS	MS	MS

TABLE 3.11. CONTINUED

1990-AUGUST SAMPLES		REGRESSION					
FUNCTIONAL GROUP/TAXON		SALMON		LAKE		COMBINED	
	±	I.W.	%WT	I.W.	%WT	I.W.	%WT
-COLLECTOR/GATHERER-	+	S	.	S	.	S	.
-FILTERER-	+	S	.	HS	HS	HS	.
-PREDATOR-	±	.	.	MS+	S-	MS+	.
-SCRAPER/GRAZER-	±	MS+	MS-	.	.	S+	.
-SHREDDER-	+	.	.	.	.	.	MS
OLIGOCHAETA	+	.	.	MS	MS	MS	MS
HYDRACARINA	+	.	.	MS	.	MS	.
DIPTERA: Ceratopogonidae	+	MS	.	MS	.	S	.
Chironomidae	+	.	.	MS	.	MS	.
Chelifera	+	.	.	MS	.	MS	.
Clinocera	+	.	.	.	.	MS	.
Prosmulium	-	.	.	.	S	.	.
Dicranota	+	.	.	HS	S	MS	.
EPHEMEROPTERA: Baetis	+	.	.	.	.	MS	.
Drunella	-	.	.	.	S	.	.
Ephemerella	+	.	.	MS	MS	S	.
Cinygmula	-	.	MS	.	MS	MS	MS
Heptagenia	+	MS	.	MS	S	S	.
Ironodes	-	.	MS	.	.	MS	S
Ameletus	+	S	.	MS	.	HS	.
PLECOPTERA: Allocapnia	+	.	MS	.	.	.	MS
Plumiperla	±	.	.	MS+	HS-	MS+	MS-
Zapada	±	.	.	MS+	S+	MS+	S-
Arcynopteryx	+	.	.	MS	MS	MS	S
Doddsia	-	.	S	.	.	.	.
TRICHOPTERA: Brachycentrus	+	S	.	.	S	MS	.
Glossosoma	+	MS	S	MS	.	S	HS
Arctopsyche	+	.	.	.	S	.	.
Hydropsyche	+	.	.	MS	MS	MS	MS
Apatania	+	S	.	MS	MS	S	.
Ecclisomyia	+	MS	.	MS	.	.	.
Onocosmoecus	+	.	.	S	S	.	.

1990-OCTOBER SAMPLES		REGRESSION					
FUNCTIONAL GROUP/TAXON		SALMON		LAKE		COMBINED	
		I.W.	%WT	I.W.	%WT	I.W.	%WT
-FILTERER-	+	S	.	HS	HS	HS	.
-PREDATOR-	-	.	.	.	S	.	.
-SCRAPER/GRAZER-	±	.	.	.	.	S+	MS-
DIPTERA: Chironomidae	-	MS	.	S	S	S	HS
Chelifera	-	.	.	S	.	S	.
Clinocera	+	.	.	S	S	S	MS
Pericoma	+	.	.	MS	.	.	.
Simulium	+	.	.	MS	.	.	.
Dicranota	+	.	MS	.	.	.	S
EPHEMEROPTERA: Drunella	-	.	.	.	S	.	.
Ephemerella	+	.	MS	.	.	.	MS
Epeorus	+	MS	.	.	.	MS	.
Heptagenia	+	.	.	S	S	S	MS
Ironodes	-	.	S	.	MS	.	S
PLECOPTERA: Allocapnia	+	MS	.	.	.	.	.
Plumiperla	-	.	.	.	.	.	.
Zapada	±	.	.	.	S+	MS-	MS+
Isoperla	+	S	.	S	.	MS	.
Doddsia	-	MS	.	.	S	MS	.
TRICHOPTERA:Brachycentrus	+	.	.	S	.	HS	.
Arctopsyche	+	S	.	S	HS	MS	S
Hydropsyche	+	.	.	S	.	.	S
Oxyethira	+	.	.	MS	MS	MS	MS
Apatania	+	S	.	MS	S	S	.
Ecclisomyia	-	S	S	.	.	MS	S
Onocosmoecus	+	.	S	.	.	.	.
TURBELLARIA	+	.	.	MS	MS	MS	MS

TABLE 3.12. Twenty macroinvertebrate taxa not included in regression analysis because they either were rarely found anywhere or were restricted to salmon and lake enriched systems.

Taxa only in enriched systems
Insecta
Diptera
Pericoma
Trichoptera
Oxyethira
Nematoda
Oligochaeta
Rhynchelmis
Pelecypoda
Sphaerium

Taxa rare to all systems
Gastropoda
Insecta
Plecoptera
Paracapnia
Neaviperla
Malenka
Nemoura
Soyedina
Arcynopteryx
Pteronarcella
Trichoptera
Amiocentris
Amphicosmoecus
Chyranda
Desmona
Eclisocosmoecus
Grensia
Hydatophylax
Limnephilius

individually in association with enrichment consistently displaying less proportional biomass. *Drunella* showed consistently greater relative biomass during the first two sampling periods and less for the last two periods. Among the heptageniid mayflies, *Ironodes* responded negatively to enrichment, while *Rithrogena* and *Heptagenia* responded positively. A stonefly, *Plumiperla*, was consistently larger in enriched systems. The trichopterans *Brachycentrus* and *Arctopsyche* responded positively to enrichment both in terms of individual size and proportional biomass.

DISCUSSION

My data show a great difference in typical macroinvertebrate community structure compared to the community structure of streams and rivers located in the same geographic region as reported by Oswood (1989). Whereas I found that Ephemeroptera and Trichoptera composed ≈80% of benthic fauna, Oswood's summation of historic data showed that Diptera dominated the benthic fauna (comprising ≈65%) in while Ephemeroptera, Plecoptera and Trichoptera were relatively rare (each averaged <10%). Although the larger than typical collecting net mesh size I employed (850 μm versus 350 μm) likely missed an unknown portion of small, early instar Chironomidae, the crux of the difference in community structure comes from my reporting the proportional biomass for each group, while Oswood summarized studies reporting the proportional number of individuals for each group. Production is the ultimate measure of a taxon's ecosystem importance from a trophic perspective (Neves 1979) but measuring it is time consuming and labor intensive. Compared to production, assessment of a

taxon's relative importance by numbers overestimates the importance of small-bodied taxa but assessment by biomass overestimates the importance of large-bodied taxa ((Hawkins and Sedell 1981). Many ecologists believe that biomass better measures the importance of a taxon in a community than density when production estimates are unavailable (Hurlburt 1971; Lyons 1981; Ludwig and Reynolds 1988). Collection of information on biomass is more time intensive because larger samples are needed to obtain sufficient biomass for obtaining accurate weights. Such data result in a better understanding of community trophic structure and the environmental factors shaping the community.

Data I collected strongly support my hypothesis that added food and nutrients from salmon runs and lake outlets have a discernible effect on community structure of stream macroinvertebrates in the oligotrophic subarctic environment of southcentral Alaska. Taxa richness and diversity both increase significantly with enrichment. The great number of statistically significant responses of orders, functional groups, and individual taxa to varying level of enrichment further supports my hypothesis. Enriched systems invariably had more Trichoptera and filter-feeders than unenriched systems. Two genera reported as extremely rare in Alaska by Oswood (1989), *Arctopsyche* and *Hydropsyche*, were common to abundant in enriched systems. *Brachycentrus*, a facultative filter-feeder, consistently showed a positive response to enrichment. Two genera of heptageniid mayflies, *Heptagenia* and *Rithrogena*, responded positively to enrichment whereas another genus, *Ironodes*, responded negatively underlining the importance of identifying organisms below family level.

More significant results occurred from lake-mediated enrichment

versus enrichment promulgated by salmon carcasses (119 versus 79). This is likely due to the more stable flow, temperature and food regime fostered by lakes in lake outlet streams when compared with the pulse of nutrients from salmon decomposition. Also, lakes likely trap nutrients from salmon runs in the lake watershed, sustaining increased production of phytoplankton and zooplankton, and so increasing the seston flow to outlet streams. The salmon escapements to these study streams were relatively small compared to runs other systems receive (Kline et al. 1989). Examining the macroinvertebrate community in streams that consistently receive large runs of salmon over large parts of the summer but do not have a lake as its source to see if the biological indices (of system enrichment) I employed approach or surpass that of lake systems would be a worthwhile study.

Although my data clearly show that lakes have a discernible effect on the macroinvertebrate communities of streams, the lake-outlet effect in Alaska may be different than generally reported (Richardson and Mackay 1991). No large concentrations of filter-feeders near lake outlets were observed. Rather, streams fed by lakes had a higher concentration of filter-feeders for kilometers downstream from the outlet. The reason for this may lie in Alaska's long and cold winters. While adult insects (gravid females) likely tend to fly upstream for oviposition in Alaska just as they do elsewhere, decreasing to occasionally nonexistent winter discharge from lakes (Robert Burrows, Water Resource Division, U. S. Geological Survey, Fairbanks, Alaska, pers. comm.) may make the initial section of lake-outlet streams inhospitable environments for winter survival for eggs and early instars of stream insects. That hostile setting can become even more

unfavorable during spring break-up. Snow-melt raises lake levels allowing large chunks of sometimes wind-driven lake ice to move through the outlet, scouring and often moving the stream substrates. These chunks of sun-weakened ice may go several hundred meters before fragmenting and ending their boulder-breaking booming bedevilment of the benthos, effectively eliminating the forum of filter feeders lying in wait for the seston of summer. Filter-feeding caddisflies in these streams have late summer emergence and reproduction flight, thus are unable to recolonize habitats that a short time after breakup become prime feeding locations. Without a large filter-feeder community at the lake outlet, seston-rich water becomes available to the whole stream.

Flowing waters have been acknowledged as constantly changing from the pre-Socratic philosopher Heraclitus (Jones 1970) to the eminent aquatic scientist Hynes (1970). Given this paradigm, I believe the nontypical, semi-quantitative method of macroinvertebrate sampling I employed, (kick-sampling large sections of stream), allowed collection of uncommonly good representations of the benthic community, although relatively large mesh size may have biased results. The typical device commonly used for benthic sampling, a Surber sampler, does yield quantitative information from the specific point that is sampled, but these data apply to a proportionally small area of the stream. This method undoubtedly misses important microhabitats where current and substrate form subtle and important gradients differentially attractive to various taxa of macroinvertebrates. Since Surber sampling was not possible in my study due to large substrates and deep water, I did not have the opportunity to compare results of both sampling

techniques so my arguments are intuitive. The results of a project comparing both sampling methods in an appropriate system would be most interesting. In such a study, one should also vary the amount of time spent collecting kick samples as I did between 1988 and 1990 (0.5 versus 1 hour). During casual field observation of the benthic communities, I believed there was a greater difference among systems in 1988 before the flood waters (with associated streambed movement) observed during 1989 and 1990. These data do not suggest as strong differences between systems during 1988 as there were during 1990. I believe the differences were there, but lesser time spent collecting the kick samples, with resulting change in sample size, is responsible for my failure to detect this change.

This study shows that relatively subtle (thus often overlooked) levels of enrichment from salmon runs and seston-rich lake discharge can have profound effects on the macroinvertebrate communities of streams in Alaska. The effects of such enrichment are likely not limited to lotic macroinvertebrates, but probably can be traced throughout the watershed (Willson 1994). These energetically richer and more diverse systems may possibly act as 'keystone' components (Mills et al. 1993) of larger ecosystems. Salmon-enriched systems may support important fish populations and terrestrial vertebrate communities, while acting as rich oases providing 'stock' for nearby more impoverished systems (Willson and Halupka in press). Further research into this phenomenon should result in natural resource managers targeting systems enriched by salmon and lake seston as important 'greater ecosystem' components in sustaining fish and wildlife production and maintaining biodiversity in Alaska.

Chapter 4---Carbon and nitrogen stable-isotope abundances in two southcentral Alaskan streams - ecological importance of salmon carcasses in lotic food webs

INTRODUCTION

The substantial role of salmon (*Oncorhynchus* spp.) carcasses in linking marine and fresh water systems has long been recognized (Juday et al. 1932, Donaldson 1967, Brickell and Goering 1970, Krokhin 1975, Richey et al. 1975). In Alaska, Kline et al (1986), Mathisen (1972), and Mathisen et al. (1988) have intensively investigated the biological enrichment of sockeye salmon systems, while Koenings and colleagues (Koenings et al. 1986; Koenings and Burkett 1987; Kyle et al. 1988) have investigated the relationships between system fertility and production of sockeye salmon. Critical ecological linkages in sockeye salmon systems differ fundamentally from systems receiving runs of other salmon species. Sockeye salmon carcasses contribute nutrients to lake ecosystems: these nutrients fertilize lake planktonic food chains supporting zooplanktivorus sockeye fry (Kline et al. in press). In contrast, other species of salmon spawning in riverine systems contribute nutrients and carbon to benthic 'biofilm' (algae and heterotrophic microbes) and to food chains based on scavenging consumers. The rapid turnover time of water in streams compared to lakes (minutes versus years) makes the importance of nutrients derived from salmon carcasses difficult to assess in streams. Retention of nutrients in an open system with unidirectional flow is the key issue. Presumably, salmon carcasses in running waters play an analogous, but diminished role in nutrient cycles compared to lake systems.

Because of difficulty in obtaining information on animal diets in

aquatic systems via observation, it is hard to construct a food web that accurately shows stream organisms connected to their important foods (Kling and Fry 1992). Examination of macroinvertebrate and contents of fish guts only provides information on ingestion of foods (not assimilation) and is restricted to recent diet (Gearing 1991). Also, unidentifiable detritus is often a significant proportion of gut contents (Chapman and Demory 1963; Gray and Ward 1979; Koslucher and Minshall 1973). Obviously, observing food-web transfers of dissolved organic carbon and plant nutrients from decomposing carcasses requires a different methodology.

Stable-isotope ratio tracers allow such a tracking of different food sources through food webs so long as the food sources have sufficiently distinct stable-isotope signatures (Hamilton and Lewis 1992; Junger and Planas 1994; Rau 1980; Rosenfeld and Roff 1992). The stable-isotope ratios in consumer tissues reflect assimilation of food sources with the carbon-isotope ratios being conservative during transfer (Rounick and Winterbourn 1986). The nitrogen-isotope ratio also indicates the trophic level of a consumer (Minigawa and Wada 1984), with an increasingly positive value (enrichment in ^{15}N compared with ^{14}N) up the trophic chain.

Stream ecologists have made extensive use of carbon-isotope ratios to trace stream food webs (e.g., Winterbourn, Cowie, and Rounick 1984; Rounick and Hicks 1985; Winterbourn, Rounick, and Hildrew 1986; Collier and Lyon 1991). In Alaska, this technique has been used to investigate planktonic trophic structure (Kling and Fry 1992). Moreover, Schell and Zieman (1989) used a combination of stable and radioactive isotopes of carbon to trace the contribution of 'old' peat carbon to freshwater and marine food webs on the

North Slope. stable-isotopes have seen limited use in investigating the flow of salmon carcass-derived carbon and nitrogen through food webs in salmon spawning streams. Kline et al. (1989) investigated coastal Sashin Creek in southeast Alaska and reported individual invertebrates and fish from salmon spawning areas to be enriched in $\partial^{15}N$ and $\partial^{13}C$ compared with those from upstream, salmon-free areas.

Macroinvertebrates function as the significant intermediary between microbiota and economically important fish. A macroinvertebrate community that receives additional energy and nutrients from salmon carcasses should potentially support more salmon fry and resident fish. The nitrogen and carbon stable-isotope ratios of salmon are generally sufficiently different from the isotope ratios of freshwater sources to allow determination of food web importance of each primary energy and nutrient source. This dissimilarity is a function of dissimilar source pools and photosynthetic pathways for carbon (Boutton 1991) along with predictable trophic enrichment between primary producers and top carnivores (DeNiro and Epstein 1981; Minigawa and Wada 1984; Fry 1988). For example, Kline et al. (1986) reported $\partial^{15}N$ and $\partial^{13}C$ values of 11‰ and -24‰ for salmon compared with averages of 0‰ and -30‰ for freshwater aquatic algae. Further evidence of significant enrichment of the system by salmon carcasses could come in two ways. First, more energy at the base of the food chain means the possibility of enough energy at the top to support additional trophic levels. Second, more energy in a heterogeneous environment would foster specialization on a particular food resources and result in a greater number of taxa. Knowing more about the contributions of salmon carcasses to stream energetics is necessary for fisheries managers concerned with declining

salmon runs (Russ Holder, Alaska Department of Fish and Game, pers. comm.) and wilderness park land managers charged with preserving natural ecosystems.

I present here a study on movement of marine-derived nutrients and energy through lotic food webs using natural abundances of $\partial^{15}N$ and $\partial^{13}C$ as tracers. I collected terrestrial and aquatic primary producers, selected stream vertebrates and proportionally representative samples of stream macroinvertebrates to evaluate the importance of salmon carcasses in the energy and nutrient flow in these southcentral Alaska river systems. I will test the hypothesis that food level transfers of carbon and nitrogen are predominately through dissolved materials to biofilm rather than direct consumption of salmon (or eggs and alevin) by scavengers.

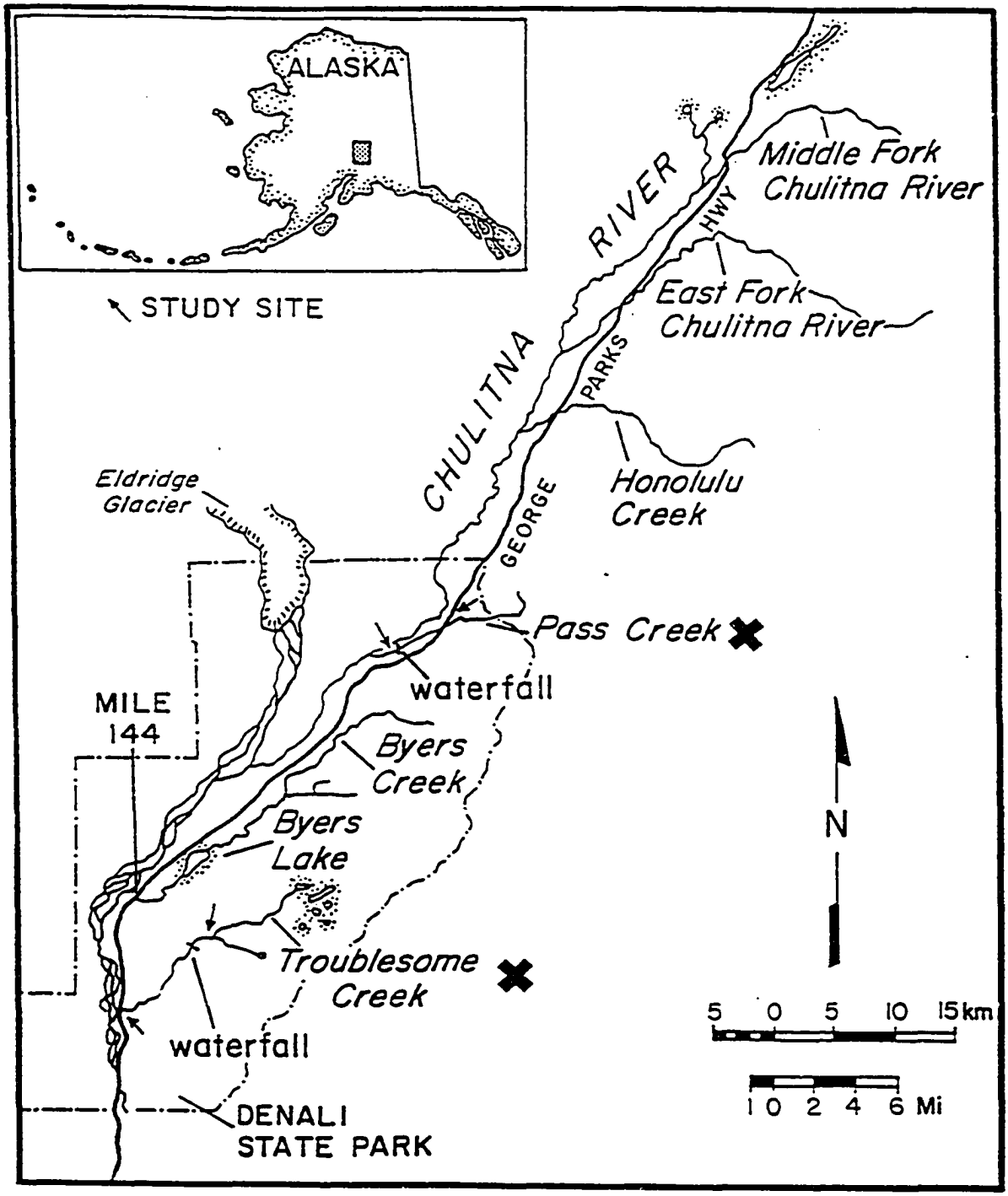
METHODS AND MATERIALS

Study sites

Lotic biota were collected from four sites on two geographically close (<20 km apart) streams. The streams are located ≈150 km NNE of Anchorage in southcentral Alaska (Figure 4.1). Study-site locations were on Lower Troublesome Creek, Upper Troublesome Creek, Lower Pass Creek, and Upper Pass Creek. These creeks were chosen because they have significant runs of salmon and provide ready accessibility from the George Parks Highway. The upper sites on each creek are inaccessible to salmon due to impassable waterfalls. These upstream reaches serve as controls.

The study streams originate from Curry Ridge in the western Talkeetna Mountains (≈1,200 m elevation). Small to large cobble are the

Figure 4.1. Map of Chulitna River Drainage in southcentral Alaska. Insert locates position of region in Alaska. Study streams, Pass Creek and Troublesome Creek, are indicated by '✖'. Sampling site locations on each study stream are delineated by arrows (⇨).



predominant stream substrates with poorly developed glacial till the predominant soil type (Tom Bundzen, Geological Survey, State of Alaska, pers. comm.). The climate of the area is maritime with the Alaska Range to the north trapping warm moist air coming in from the North Pacific Ocean. Seasonal precipitation can exceed 125 cm water equivalent with snowfalls of >9 m not uncommon (R. Ostermick, Ermine Lake resident, pers. comm.). Unlike Interior Alaska, extremely cold winter temperatures (<-17°C) are rare though ice forms on the rivers in October with breakup ending in late May. During 1988, summer water temperatures reached 18°C during August. I estimated that approximately 1,500 degree days (above 0°C) accumulated for the study streams that year based on average readings taken every two weeks from min-max thermometers situated in Byers Creek, Honolulu Creek, Pass Creek, and Troublesome Creek.

All watersheds are free from significant anthropogenic disturbance. The vegetation is dominated by white birch (*Betula papyrifera*) and poplar (*Populus tacamahacca*) with occasional white spruce (*Picea glauca*). Thick willow (*Salix* spp.) and alder (*Alnus* spp.) stands dominate riparian zones.

Watershed areas are 54 km^2 for Pass Creek and 98 km^2 for Troublesome Creek with stream gradients ranging from 10 m/km to 30 m/km for the 3 km above each study site. Elevations for these sites ranged from 180 m to 380 m. Average baseflow discharge during July, August, and September of 1993 was similar at all sites on both third order creeks, ranging from $\approx$1.5 $m^3 \cdot sec^{-1}$ to $\approx$3.0 $m^3 \cdot sec^{-1}$. Spawning habitat is relatively concentrated on Pass Creek along $\approx$1.5 km of stream length. This contrasts with the spawning habitat of Troublesome Creek being scattered over $\approx$10 km.

Accurate historic data on strength of salmon runs to these creeks is

unavailable but both study streams have escapements of variable size. Despite difficult survey conditions, low stream levels in 1988 allowed for an approximate estimate of run size that year. King salmon escapement was estimated at ≈1,000 fish for both creeks as was chum and silver salmon escapement for Troublesome Creek. Pass Creek received an order of magnitude less chum and silver salmon along with≈200 pink salmon. Troublesome Creek received ≈5,000 pink salmon. No estimates of salmon escapement were made in 1989 and 1990 due to continually high stream discharge. There was an unusual plethora of salmon smolts in stomachs of rainbow trout caught in June 1990 from Troublesome Creek. Because no such phenomenon was noted in June 1988 or June 1989, the 1989 escapement of chum and pink salmon to Troublesome Creek was probably higher than that of 1988 .

The salmon run in Troublesome Creek in 1988 resulted in an estimated gross fertilization of ≈2 gm $N \cdot m^{-2}$ of streambed ((≈1.6 x 10^7 gm fish biomass x ≈2% N)/(≈1 x 10^4 m stream length x 15 m stream width)). The salmon run in Pass Creek in 1988 resulted in an estimated gross fertilization effect of ≈10 gm $N \cdot m^{-2}$ of streambed ((≈7.7 x 10^6 gm fish biomass x ≈2% N)/(≈1.5 x 10^3 m stream length x 10 m stream width)). This input occurred over a period of approximately 90 days (July 1 to October 1).

The yearly cycle of the salmon runs start with king/chinook salmon (*O. tshawytscha*) entering streams by the middle of June. Peak spawning activity occurs from late June through early July with most fish dead and decomposed by the end of July. Dog/chum salmon (*O. keta*) and pink/humpy salmon (*O. gorbuscha*) enter the creeks during early August,

spawning and dying by that month's end. Silver/coho salmon (*O. kisutch*) spawn from mid-August through mid-September with rare individuals still alive and spawning in early October.

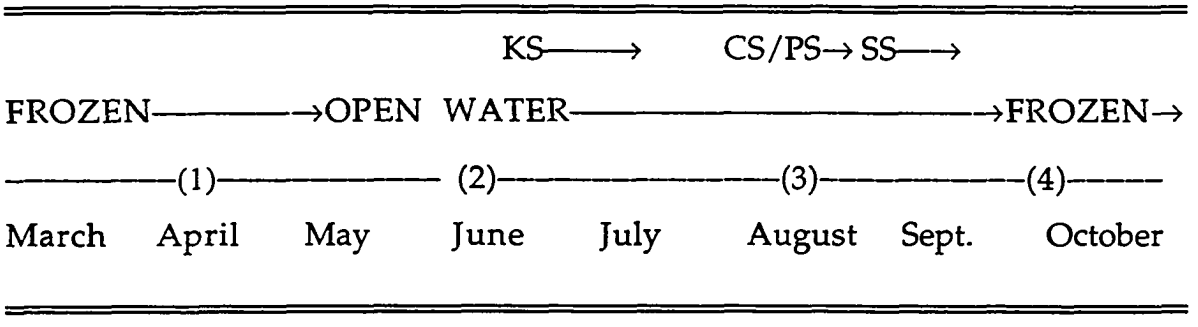
Sampling protocol

Sampling sites on both study creeks were established above and below the waterfall on each creek. Because these waterfalls were a barrier to upstream migration of salmon, the effects of the presence of salmon on each system could be evaluated. Specifically, one site on each study stream was established near the George Parks Highway, another sampling site was established 3 km downstream from the highway below a 30-m waterfall on Pass Creek, and a fourth sampling site was located 10 km upstream from the highway above a 5-m waterfall on Troublesome Creek.

Samples were collected during four ecologically different periods during both 1988 and 1990 to assess seasonal changes in stream energetic and nutrient inputs. These times were pre-breakup, while the streams were mostly frozen (late April), post break-up and pre-salmon (mid-June), middle of salmon runs (mid-August), and post salmon runs (early October) (Figure 4.2). All samples for each period were collected during 2 days of stable weather to limit stormflow-induced variations in communities of benthic macroinvertebrates.

Freshly fallen leaves (unprocessed by macroinvertebrates) from riparian trees were collected from streams in September. Algae, primarily filamentous green algae, was 'snipped' off benthic rocks at each site when available and constituted relatively pure algae, substantially free of microorganisms and detritus. Sewage fungus complex (SFC), a community of

Figure 4.2. Monthly phenology of sampling protocol in relationship to salmon spawning activities and stream ice cover. Upper case letters indicated spawning period for each salmon species utilizing creek (KS=king salmon, CS=chum salmon, PS=pink salmon, and SS=silver salmon). Numbers in parentheses indicate sampling period.



filamentous algae, filamentous bacteria and fungi, was collected from the benthos and scraped off a salmon carcass.

Macroinvertebrate samples were collected in 1988 and 1990 using a rectangular (460 mm x 200 mm) Bottom Aquatic Kick Net (mesh: 800 µm x 900 µm) from WildCo Supply Co., Saginaw, Michigan. Each sample site was approximately 50 m long and stream-width wide, encompassing representative microhabitats (runs, riffles, pools, and large woody debris). While holding the net downstream from myself, I kicked and scraped all substrate to a depth of ≈10 cm while moving down the length of each study stretch. This was repeated along lines parallel to the first collecting course. This sampling technique provided semi-quantitative data (information on relative, but not absolute, abundance of benthic invertebrate taxa). Semi-quantitative sampling of the entirety of large reaches (50 m) containing representative microhabitats had two advantages: (1) sampling of such a very large area provided the large biomass necessary for isotope determinations of individual taxa; and, (2) conventional quantitative samplers (e.g., Surber sampler) would have been unusable in the common deepwater and large substrate microhabitats. In 1988, approximately 0.5 hour was spent collecting each sample. After analysis of 1988 data showed dry biomass of the most abundant macroinvertebrate taxa collected was marginal (<10 mg) for determining isotope ratios with equipment then available, approximately 1 hour was spent collecting each sample in 1990.

No attempts were made to clear insect guts. Samples were frozen within several hours after collection. The protocol for (Mihuc and Toetz 1994) and the necessity of clearing insect guts is questionable. Junger and Planas (1994) found that macroinvertebrates did not completely clear their guts even

after 2 days in clean water. More importantly, they noted no significant isotopic difference between insects with or without 'cleared' guts.

In the laboratory, benthic samples were thawed. Macroinvertebrates were removed from associated detritus using a WILD [Model Five] dissecting microscope. All macroinvertebrates from 1988 were identified at least to family whereas macroinvertebrates from 1990 were identified to genus when possible using the classifications of Merritt and Cummins (1978), Stewart and Stark (1988), and Wiggins, (1977). Functional group classifications of taxa were taken from Merritt and Cummins (1978) and verified through limited gut analysis. Taxa from each sample were separated, counted and air-dried for 1 week. Each dessicated taxon (from 1 to >200 individuals) was then weighed to the nearest milligram (ranged from <1 mg to >200 mg). A 'Wiggle-Bug Amalgamator' (Crescent Dental Manufacturing, Chicago, Illinois) was used to grind each taxon group into a powder. The advantage of using composite samples (many individuals of one taxon) is that they better reflect group isotope composition (Kling and Fry 1992).

Sculpins (*Cottus cognatus*) and salmon fry were a by-catch of macroinvertebrate sampling. Salmon fry were also captured using minnow traps. Sport fishing methods were employed to capture all species of salmon, rainbow trout (*O. mykiss*) and grayling (*Thymallus arcticus*). American dippers (*Cinclus mexicanus*) were collected with a shotgun. Small fish were ground whole for stable-isotope analysis. In larger fish and American dippers, a section of muscle was dissected, dried and ground.

Analysis was done at the Institute of Marine Science, University of Alaska, Fairbanks, using a EUROPA Model 20-20 stable-isotope Analyzer. By

convention, carbon and nitrogen-isotope ratios are expressed as parts per thousand difference between Peedee Belemnite carbon and atmospheric nitrogen, respectively, using the following equation: $\partial^{15}N$ or $\partial^{13}C$ (‰) = $[(R_{sample}-R_{standard})/R_{standard}] \times 10^3$ where R is ($^{15}N/^{14}N$) or ($^{13}C/^{12}C$). Duplicate analyses on the same sample consistently differed by <0.5‰.

Statistical analysis

The computer program STATVIEW© (Abacus Concepts, Berkeley, California) was used to analyze data. Isotope ratios of organisms downstream versus upstream of waterfalls (ie. presence or absence of salmon) were compared using a parametric unpaired t-test. Test results (p values) are reported in the following manner; between 0.10 and 0.05 as marginally significant, between 0.05 and 0.01 as significant, and < 0.01 as highly significant. Statistical analyses (t-tests) were not corrected for experiment-wide error rate; exploratory data analysis was of greater importance than maintaining tight control of type I error across all analyses.

RESULTS

Terrestrial and aquatic vegetation and aquatic heterotroph

The algal samples collected displayed much variability, with individual sample $\partial^{13}C$ values ranging from -17.81 to -36.81. The average $\partial^{15}N$ algal value for stream sites below waterfalls (with spawning salmon) was more enriched than for stream sites above waterfalls (no spawning salmon) although there was no statistically significant difference (Table 4.1). The average $\partial^{13}C$ algal value in lower stream sites was more depleted than in upper stream sites although again there was no statistically significant difference (Table 4.1). The average isotopic composition for all algal samples

TABLE 4.1. $\partial^{15}N$ and $\partial^{13}C$ values for epilithic algae in Pass Creek and Troublesome Creek (mean±1 SE: n=number of samples).

Isotopes	Lower Pass Creek (n=4)	Upper Pass Creek (n=4)	P-value (t-test)
$\partial^{15}N$	1.81 (1.05)	0.96 (1.25)	n.s.
$\partial^{13}C$	-26.14 (1.55)	-24.69 (6.70)	n.s.
	Lower Troublesome Creek (n=3)	Upper Troublesome Creek (n=1)	
$\partial^{15}N$	1.43 (1.56)	-0.26	n.s.
$\partial^{13}C$	-28.89 (4.69)	-25.20	n.s.

was 1.44±1.25(SE) $\partial^{15}N$ and -26.92±4.49(SE) $\partial^{13}C$. Overall, epilithic algae, (both biofilm and filamentous) was consistently sparse to nonexistent at all sampling sites despite a relatively open canopy. This made collection of adequate sample size for determining spatial and temporal variation in isotopic composition of both types of algae not feasible.

Isotope values for sewage fungus complex (SFC) ranged from -0.04 to 10.25 for $\partial^{15}N$ (average 3.66) and -17.12 to -24.98 for $\partial^{13}C$ (average -21.55) (n=10). Isotope values for SFC taken off an submerged decomposing salmon carcass were 12.11 for $\partial^{15}N$ and -23.05 for $\partial^{13}C$.

Aquatic moss ooccurred in limited quantities only at the sampling site in Upper Troublesome Creek. Aquatic moss is not thought to be a significant food source for stream consumers (Hynes 1970). The average isotopic composition for three moss samples was comparatively depleted with $\partial^{15}N$=-0.66±0.86(SE) and $\partial^{13}C$=-29.39±2.41(SE).

The dominant taxa of the riparian-zone vegetation contributing leaves to stream food webs were willow, alder, poplar, and birch. The average value for leaves from the four taxa is $\partial^{15}N$=-2.30±0.61(SE) and $\partial^{13}C$=-28.32±0.70(SE) (Table 4.2).

Aquatic macroinvertebrates

Four benthic samples were taken at each site in both 1988 and 1990. Increased collection effort per sample in 1990 resulted in both the average number of macroinvertebrates collected per sample and their dry biomass to more than double compared with samples from 1988. Despite this increased effort, the average dry weight per individual macroinvertebrate per sampling period changed little between the 2 years (Table 4.3). This indicates that increased sampling effort targeted macroinvertebrates of similar size.

TABLE 4.2. $\partial^{15}N$ and $\partial^{13}C$ values for leaves of trees and shrubs common to the watersheds of Pass Creek and Troublesome Creek.

	$\partial^{15}N$‰		$\partial^{13}C$‰	
	Mean	S.E	Mean	S.E
Willow (n=9)	-3.46	1.12	-28.38	0.49
Alder (n=7)	-2.31	0.38	-27.67	0.88
Poplar (n=8)	-2.03	0.66	-28.49	0.67
Birch (n=3)	-1.54	0.28	-28.74	.077
Average of all leaf taxa (n=4)	-2.30	0.61	-28.32	0.70

TABLE 4.3. Average macroinvertebrate numbers and dry weights for benthic samples collected at four sample sites on Troublesome and Pass Creeks in 1988 and 1990. (mean ±1 SE: n=number of samples)

	1988 (n=16)	1990 (n=16)
Total macroinvertebrates collected	14,745	42,554
Average number of individual macroinvertebrates per sample	922±324 (range: 160-3631)	2660±555 (range: 750 to 4624)
Total macroinvertebrate dry biomass collected	8,383 mg	16,967 mg
Average dry macroinvertebrate biomass per sample	487±123 mg (range: 151 to 1027)	1060±232 mg (range: 151 mg to 2728 mg)
Average dry weight per individual macroinvertebrate per sample	0.49±0.32 mg. (range: 0.16 to 5.52)	0.46±0.18 mg. (range: 0.17 to 1.82)

Carbon and nitrogen-isotope ratios were determined for an average of 10 common taxa per site per sampling period (4 times a year for 2 years at four sites ≈320 values) (Appendix B). Two taxa, (with adequate biomass for analysis) from each of the five functional groups were usually represented in these 10 taxa. The groups were collector-gatherers, scrapers, predators, shredders and filter-feeders (Merrit and Cummins 1978). These isotopic determinations were made on taxa samples collectively representing an average of 91.48%±3.94%(SE) of all macroinvertebrate biomass collected per sampling period. Because benthic collections were representative of each macroinvertebrate community at a particular time and isotope ratios were determined for representatives of the dominant taxa in the communities, this information was used to calculate (using weighted averages) a whole macroinvertebrate community isotopic value for each time period for each site (Table 4.4).

I observed significant differences in $\partial^{15}N$ values between Lower and Upper Troublesome Creek in 1990, between Lower and Upper Pass Creek in 1988 and between years for Lower Troublesome Creek. Lower sites were isotopically more enriched. The $\partial^{13}C$ values varied significantly between Lower and Upper Troublesome Creek in 1990 (lower site more enriched). All four study sites varied between years with heavier values in 1988 (Table 4.5).

The average annual range between the isotopically most enriched and least enriched macroinvertebrate taxa in both $\partial^{15}N$ and $\partial^{13}C$ values per sampling period was calculated to assess effects of salmon carcasses on isotope values of consumers. There was no statistically significant difference in average ranges per sampling period for $\partial^{15}N$ values between lower and upper sites on each creek (Table 4.6). The June 1990 collection of macroinvertebrate

TABLE 4.4. Calculated $\partial^{15}N$ and $\partial^{13}C$ values of macroinvertebrate communities in Pass and Troublesome Creeks in 1988 and 1990. (Ave= mean ±1 SE)

	LOWER PASS CREEK		UPPER PASS CREEK	
	$\partial^{15}N$‰	$\partial^{13}C$‰	$\partial^{15}N$‰	$\partial^{13}C$‰
1988-April	3.96	-30.45	3.02	-36.56
June	3.13	-29.03	1.27	-36.34
August	3.94	-29.33	2.82	-34.84
October	4.49	-28.78	3.81	-34.11
1988-Ave	3.88±0.28	-29.40±0.37	2.73±0.53	-33.40±1.07
1990-April	5.68	-33.06	2.25	-37.37
June	4.53	-31.25	2.27	-34.57
August	2.64	-30.79	1.10	-32.82
October	5.52	-33.06	4.35	-32.84
1990 Ave.	4.59±0.70	-32.04±0.60	2.59±0.68	-34.40±1.07
	LOWER TROUBLESOME CREEK		UPPER TROUBLESOME CREEK	
1988-April	1.72	-28.76	1.61	-27.49
June	1.5	-27.33	1.25	-27.89
August	0.54	-26.31	1.10	-27.47
October	2.73	-26.24	2.63	-26.42
1988-Ave	1.62±0.45	-27.16±0.59	1.65±0.34	-27.32±0.31
1990-April	4.62	-28.07	3.35	-29.02
June	4.25	-30.18	2.38	-28.20
August	3.43	-26.57	1.01	-25.32
October	3.81	-26.67	1.77	-26.57
1990 Ave.	4.03±0.26	-27.87±0.84	2.13±0.49	-27.28±0.83

TABLE 4.5. Statistically significant differences between lotic macroinvertebrate community isotope values for Upper and Lower Troublesome Creek and Upper and Lower Pass Creek for 1988 and 1990.

	$\partial^{15}N$ p-value (n = 4)	$\partial^{13}C$ p-value (n = 4)
Lower versus Upper Troublesome Creek 1990	0.0325	0.0012
Lower versus Upper Pass Creek 1988	0.0144	n.s.
Lower Troublesome Creek 1988 versus 1990	0.0053	0.0039
Upper Troublesome Creek 1988 versus 1990	n.s.	0.0002
Lower Pass Creek 1988 versus 1990	n.s.	0.0100
Upper Pass Creek 1988 versus 1990	n.s.	0.0112

TABLE 4.6. Ranges in stable-isotope values between least and most enriched lotic macroinvertebrate taxa collected at Troublesome Creek and Pass Creek sites during 1988 and 1990 (n = 4).

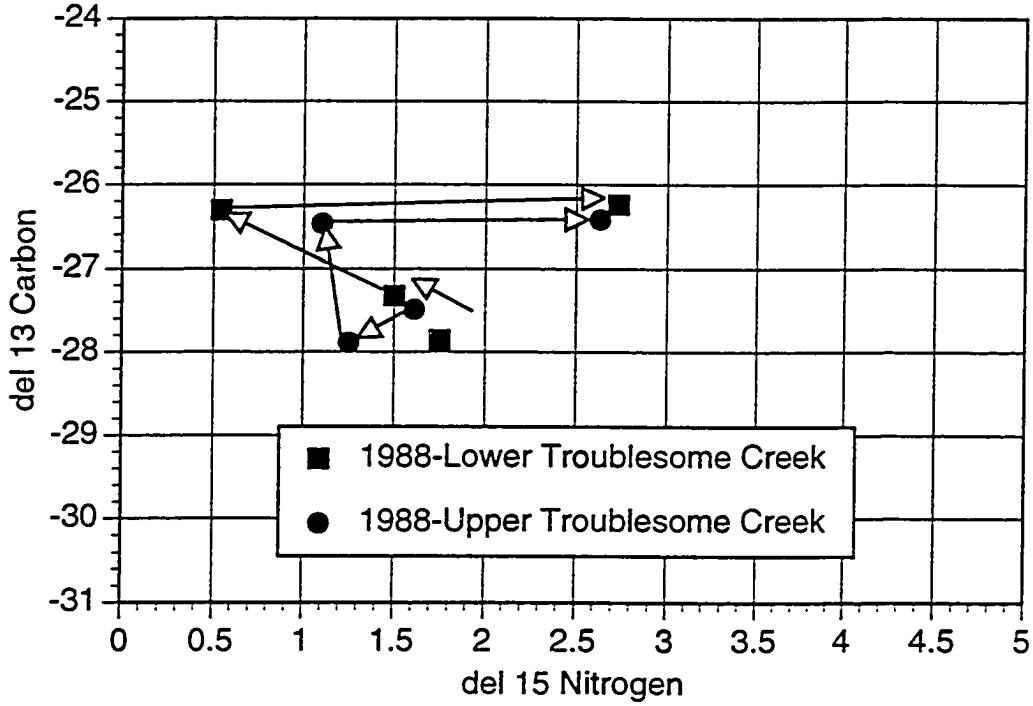
	1988			1990		
	Lower Pass Creek	Upper Pass Creek	P value	Lower Pass Creek	Upper Pass Creek	P value
$\partial^{15}N‰$	2.81	2.40	n.s.	5.65	4.61	n.s.
$\partial^{13}C‰$	3.67	5.76	0.006	8.65	10.88	n.s
	1988			1990		
	Lower Troublesome Creek	Upper Troublesome Creek	P value	Lower Troublesome Creek	Upper Troublesome Creek	P value
$\partial^{15}N‰$	4.01	4.24	n.s	4.95	3.24	n.s
$\partial^{13}C‰$	4.38	3.94	n.s	5.22	5.43	n.s

taxa from both Lower Troublesome Creek and Lower Pass Creek showed the largest range of $\partial^{15}N$ values from least enriched to most enriched taxa. These ranges were 8.72‰ and 8.96‰, respectively. Unfortunately, high-water conditions during August and September 1989 prevented surveys of salmon runs that could suggest a causal relationship. The least enriched ($\partial^{15}N$) taxon at both sites in June 1990 was a collector-gatherer mayfly (Ephemeroptera: Ephemerellidae-*Ephemerella*). The isotopically most enriched taxon at both sites was a predatory stonefly (Plecoptera: Chloroperlidae-*Plumiperla*). There was no statistical difference in average annual ranges of $\partial^{13}C$ values for macroinvertebrate taxa between lower and upper sites on Troublesome Creek during 1988 and 1990. Upper Pass Creek had statistically significant greater ranges than did Lower Pass Creek in 1990 (Table 4.6).

Data displayed a consistent seasonal trend in community isotope values for both years. Values of $\partial^{13}C$ were lowest in April and June samples and highest in August and October samples. The $\partial^{15}N$ values were high in the spring, lowest in August and high again by October (Figures 4.3a, 4.3b, 4.4a, 4.4b)

The $\partial^{13}C$ and $\partial^{15}N$ values of the macroinvertebrate taxa that had both regular and adequate presence at sampling sites usually displayed seasonal cycling similar to that displayed by the macroinvertebrate community considered as a whole (Figures 4.5a, 4.5b, 4.5c). A trichopteran (*Arctopsyche*) in salmon-enriched Lower Troublesome Creek showed a distinct lack of typical seasonal cycling. *Arctopsyche*, a net-spinning caddisfly, constructs large mesh capture nets and largely consumes animal seston. The tracking of seasonally predominant food resources by *Arctopsyche*, (April-algae, June-salmon smolts, August-algae, October-salmon), rather than the circular

FIGURE 4.3a, 4.3b. Seasonal changes in macroinvertebrate community isotope values for Upper and Lower Troublesome Creek-1988 and 1990. Arrows indicate direction of bimonthly changes.



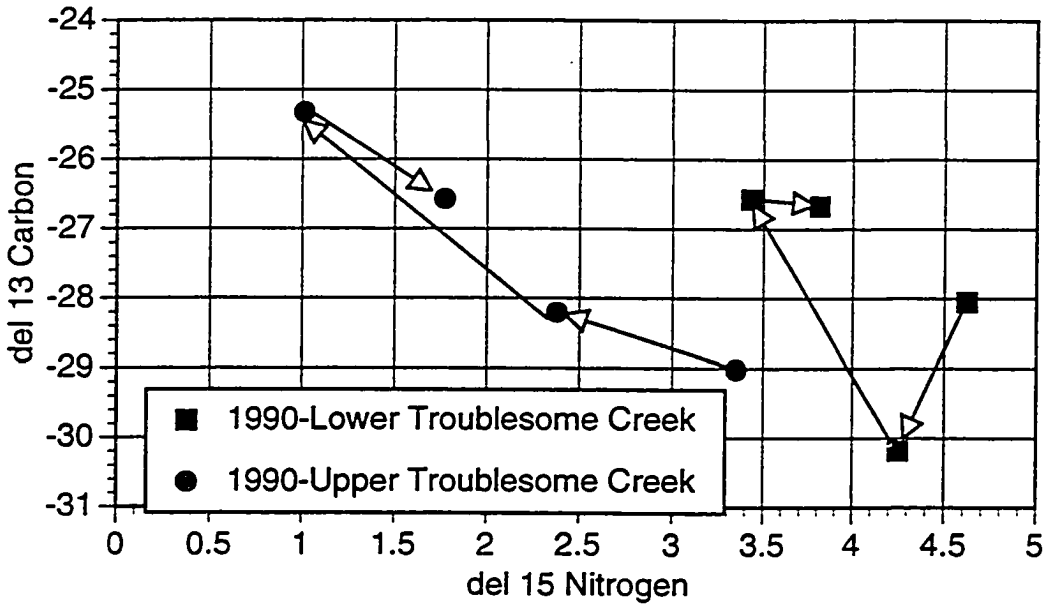


FIGURE 4.4a, 4.4b. Seasonal changes in macroinvertebrate community isotope values for Upper and Lower Pass Creek-1988 and 1990. Arrows indicate direction of bimonthly changes.

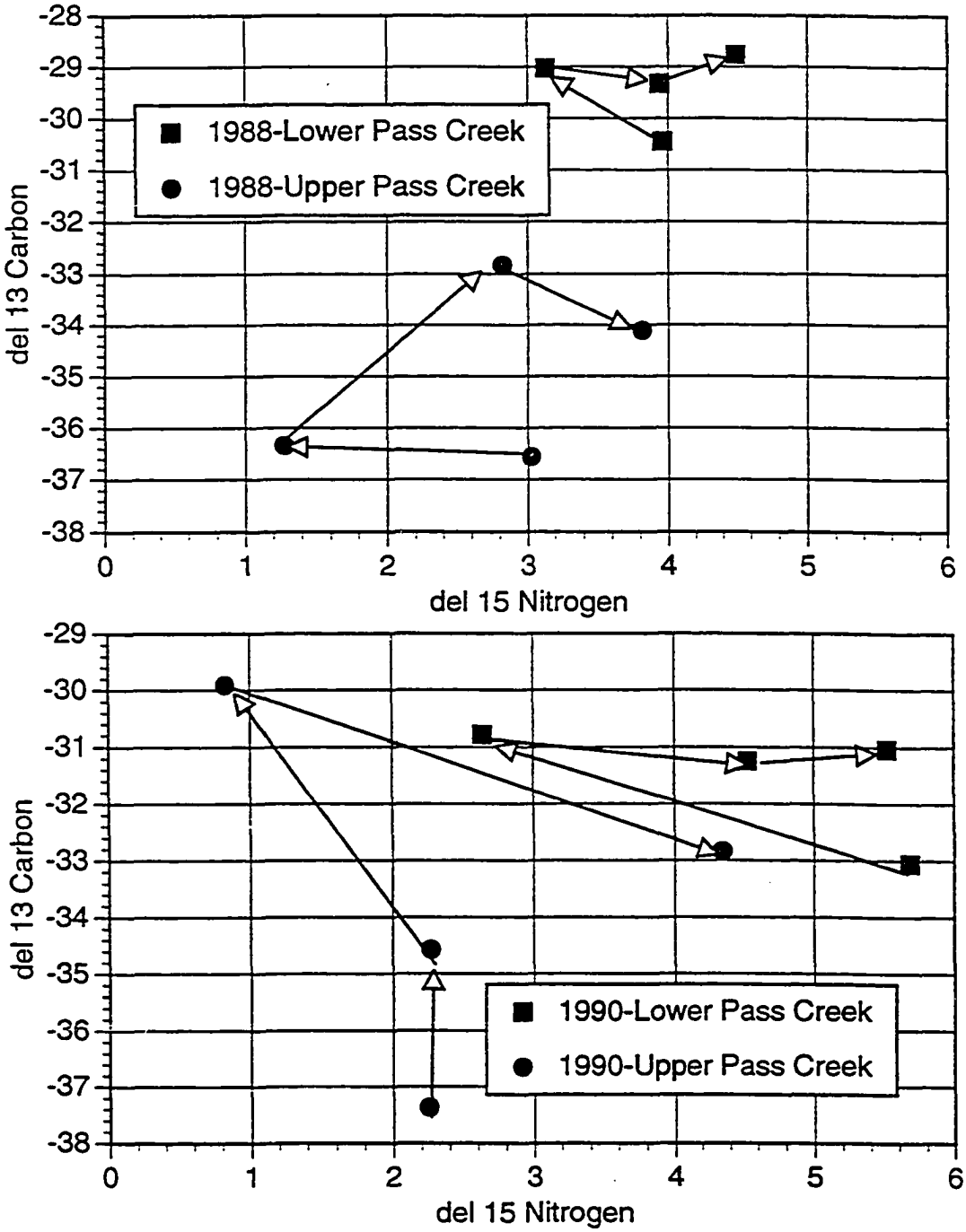


FIGURE 4.5a. Seasonal changes in isotope values for *Brachycentrus* and *Ephemerella*. Arrows indicate direction of bimonthly changes. (LT = Lower Troublesome Creek, UT = Upper Troublesome Creek, LT = Lower Pass Creek, UT = Upper Pass Creek).

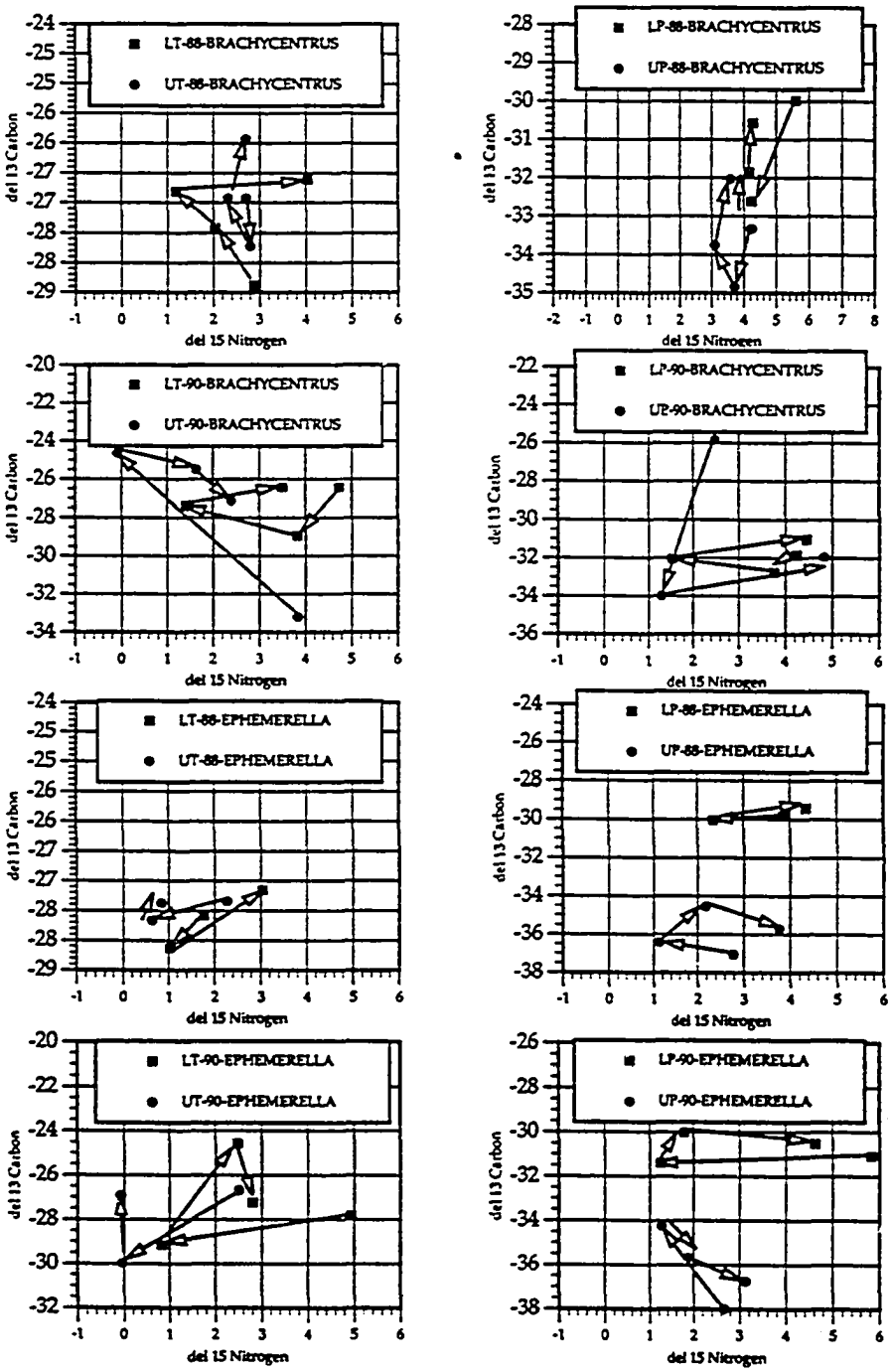


FIGURE 4.5b. Seasonal changes in isotope values for *Drunella*, *Glossosoma*, and Heptageniidae. Arrows indicate direction of bimonthly changes. (LT = Lower Troublesome Creek, UT = Upper Troublesome Creek, LT = Lower Pass Creek, UT = Upper Pass Creek).

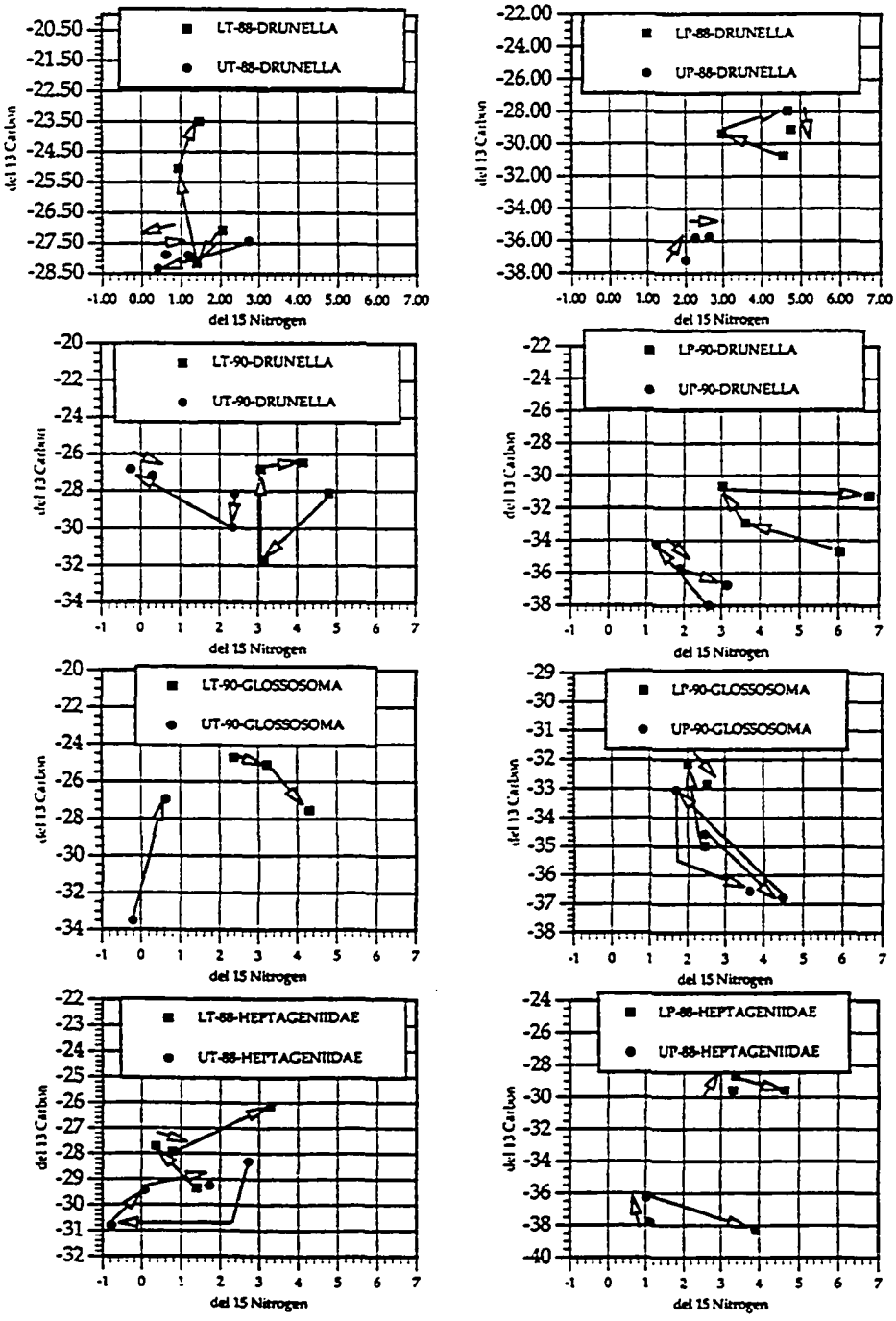
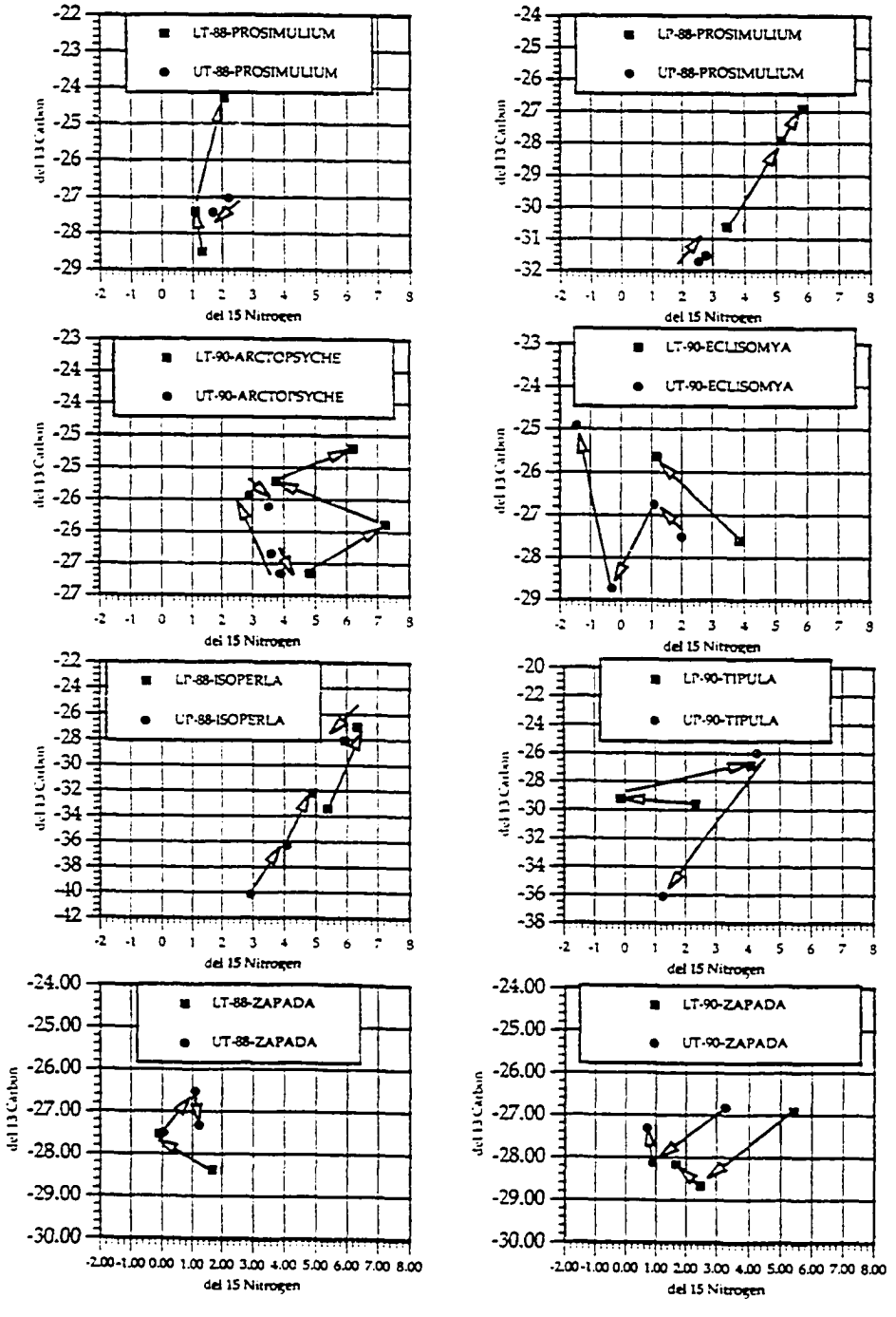


FIGURE 4.5c. Season changes in isotope values for *Arctopsyche, Ecclisomyia, Isoperla, Prosimulium, Tipula,* and *Zapada.* Arrows indicate direction of bimonthly changes. (LT = Lower Troublesome Creek, UT = Upper Troublesome Creek, LT = Lower Pass Creek, UT = Upper Pass Creek).



pattern display by other macroinvertebrates, may be the result of a suspected semi-voltine life history cycle with late instar larvae always present.

In 1988, the average annual $\partial^{15}N$ and $\partial^{13}C$ values for each of six macroinvertebrate taxa occurring regularly at both lower and upper sites on Troublesome Creek were not statistically different between sites. In 1990, four of nine taxa displayed average $\partial^{15}N$ values that were significantly heavier at the lower site while there was no difference in $\partial^{13}C$ values. One of six taxa from the lower site had significantly heavier average annual $\partial^{15}N$ values in 1990 compared with 1988. In 1988, the annual average $\partial^{15}N$ values for two of seven macroinvertebrate taxa occurring regularly at both lower and upper sites on Pass Creek was significantly heavier at the lower site. That same year, four of seven taxa at the lower site were significantly heavier in $\partial^{13}C$ values compared to the upper site. In 1990, two of five taxa displayed average $\partial^{13}C$ values that were significantly heavier at the lower site while there was no difference between sites for any of the five taxa in $\partial^{15}N$ values. One of five taxa from the lower site had significantly heavier $\partial^{13}C$ values in 1990 compared to 1988 (Table 4.7).

Pre-pupal larvae of blowflies (Family: Calliphoridae) obtained from a carcass of a king salmon exposed in a riffle were used to determine how close the isotope values of these macroinvertebrates were to the isotopic values of their food (salmon carcasses). This was the only direct measurement of fractionation values for watershed biota eating salmon carcasses. The $\partial^{15}N$ value of 16.06 and the $\partial^{13}C$ value of -18.75 for these maggots represent an enrichment of $\approx$1‰ for carbon and slightly more than 1‰ enrichment for ∂^{15} nitrogen.

TABLE 4.7. Significant differences in stable-isotope composition between sites and years for individual macroinvertebrate taxa (n = 3 or 4 per site/year) from Pass and Troublesome Creeks. In all cases, the isotopically heavier taxa came from the salmon carcass enriched lower sampling sites.

Location/year	Taxon	$\partial^{15}N$ P-value	$\partial^{13}C$ P-value
L. Troublesome versus U. Troublesome 1990	Ephemeroptera: Ephemerellidae-*Drunella*	0.04	n.s.
	Trichoptera: Hydropsychidae-*Arctopsyche*	0.040	n.s.
	Glossosomatidae-*Glossosoma*	0.029	n.s.
	Rhyacophilidae-*Rhyacophila*	0.035	n.s.
L. Troublesome 1988 versus 1990	Ephemeroptera: Ephemerellidae-*Drunella*	0.0027	n.s.
L. Pass versus U.Pass 1988	Ephemeroptera: Ephemerellidae-*Drunella*	0.031	0.0003
	Ephemerella	n.s.	0.0002
	Heptageniidae	n.s.	0.0003
	Plecoptera: Perlodidae-*Isoperla*	0.04	n.s.
	Trichoptera: Brachycentridae-*Brachycentrus*	n.s.	0.037
L. Pass versus U.Pass 1990	Ephemeroptera: Ephemerellidae-*Drunella*	n.s.	0.02
	Ephemerella	n.s.	0.0007
L. Pass 1988 versus 1990	Ephemeroptera: Ephemerellidae-*Drunella*	n.s.	0.02

Vertebrates

The isotopic composition of adult salmon varied depending upon species (Table 4.8). King salmon that spend three to five years feeding in the marine environment were significantly heavier ($p<0.05$) in both nitrogen and carbon than all other salmon species. Pink, coho and chum were similar isotopically. The average $\partial^{15}N$ for the four species of salmon was 12.53±1.30(SE) and the average $\partial^{13}C$ was -20.90±1.23(SE). Infertile salmon eggs (species unknown, n = 5) collected from the benthos during October averaged 13.06±1.56(SE) $\partial^{15}N$ and -22.52±0.62(SE) $\partial^{13}C$. Salmon alevin (species unknown, n = 6) collected in April were 13.99±1.32(SE) $\partial^{15}N$ and -24.03±2.72(SE) $\partial^{13}C$. Salmon fry (coho, n = 5) from July were lighter (8.08±0.27(SE) $\partial^{15}N$ and -26.23±0.54(SE) $\partial^{13}C$) than the alevin stage. Salmon fry (n = 4) became heavier (11.70±0.86(SE) $\partial^{15}N$ and -24.94±1.39(SE) $\partial^{13}C$) by October though they were still isotopically lighter than salmon eggs.

The changes in isotopic values for carcasses of chum salmon deteriorating in-stream were measured (See Chapter 2). Thirteen unspawned chum salmon were collected. Four were frozen for later isotope analysis. The remaining nine were attached to the benthos of a stream. After one month in the stream at 0°C, the fish had lost an average of 40% of their biomass, predominately through microbial decomposition. Their remaining flesh averaged 13.04±0.69(SE) for $\partial^{15}N$ and -21.49±0.77(SE) for $\partial^{13}C$. This is 1.5±0.69(SE) heavier for $\partial^{15}N$ and 1.2±0.77(SE) lighter for $\partial^{13}C$ than average fresh chum flesh (n = 4).

Sculpin generally displayed little seasonal isotopic variation (Figures 4a, 4b) averaging 6.75±0.45(SE) $\partial^{15}N$ and-27.31±1.06(SE) $\partial^{13}C$ over all sites for all seasons and years. Although this average seasonal variation was ≈0.5‰ for $\partial^{15}N$, sculpin on L. Pass Creek in 1988 and L. Troublesome Creek in 1990

TABLE 4.8. $\partial^{15}N$ and $\partial^{13}C$ values of four species of adult anadromous salmon, decomposing chum salmon, loose salmon eggs, recently emerged fry and <1 year old fry. (mean ±1 SE: n = number of samples)

	$\partial^{15}N$‰	$\partial^{13}C$‰
King salmon n=11	14.60±0.48	-19.02±0.79
Chum Salmon (Fresh) n=4	11.51±0.48	-20.3±0.18
Chum Salmon (1 month old) n=9	13.04±0.69	-21.49±.077
Coho salmon n=3	11.68±1.1	-21.83±0.36
Pink Salmon n=5	11.85±0.58	-21.86±0.44
Loose salmon eggs n=5 (3 eggs each)	13.06±0.75	-22.52±0.31
Recently emerged fry (April) n=2	13.99±0.61	-24.03±1.36
< one-year old coho fry (July) n=5	8.08±0.27	-26.23±0.54
< one-year old coho fry (October) n=4	11.70±0.86	-24.94±1.39

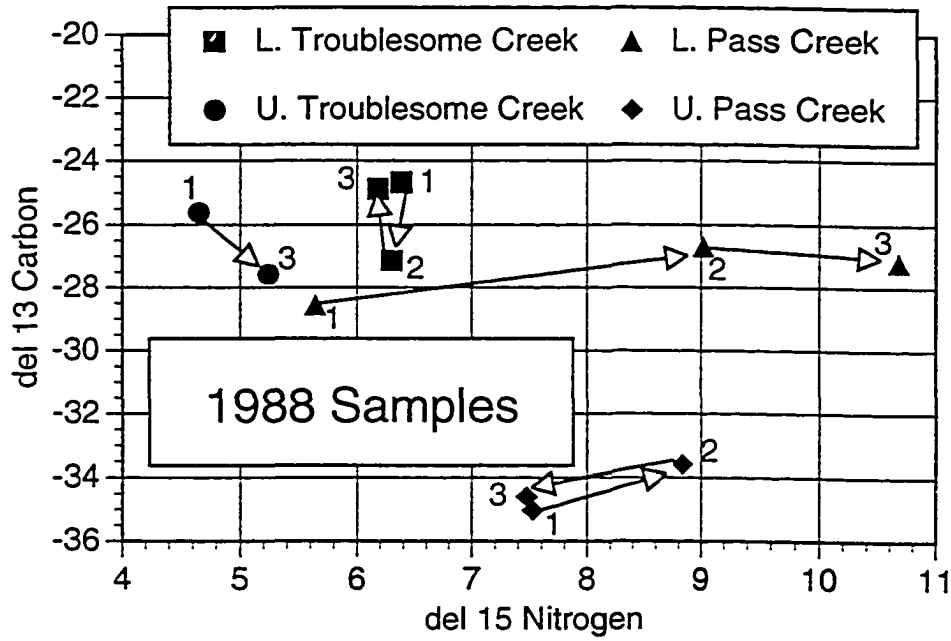
became enriched in $\partial^{15}N$ during the summer by 5.5‰ and 1.6‰, respectively (Figures 4.6a, 4.6b). This was up to an order of magnitude increase compared to sculpin above waterfalls (no salmon). There was little isotopic difference between different age classes (young-of-year, ≈1 year, >1 year) of sculpin during October 1987 with $\partial^{15}N$ values of 9.54, 9.31, 9.51 and $\partial^{13}C$ values of -25.27, -26.05, -25.56 respectively.

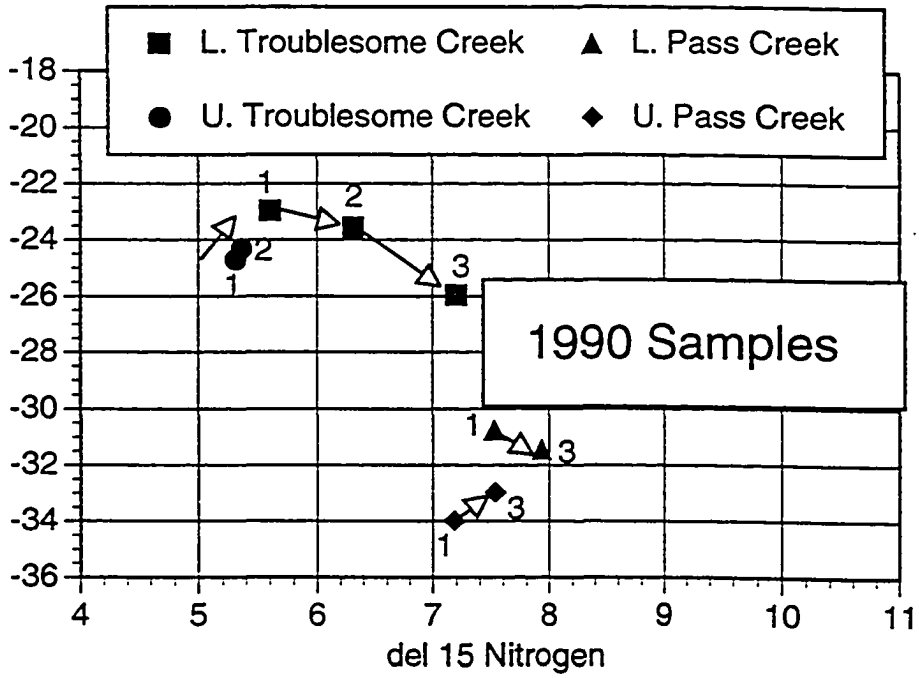
Grayling and rainbow trout did not inhabit reaches of the study streams above waterfalls, therefore obtaining control isotopic values for these species was impossible. Grayling collected below the waterfall on Pass Creek in June averaged 10.18±0.50(SE) $\partial^{15}N$ and -25.67±1.03(SE) $\partial^{13}C$ (n = 3). Grayling collected below the waterfall on Pass Creek in August became heavier averaging 11.40±0.87(SE) $\partial^{15}N$ and -24.57±0.09(SE) $\partial^{13}C$ (n=3).

Rainbow trout were the heaviest stream resident isotopically, averaging slightly more enriched in June than salmon-derived nitrogen (14.16±0.24(SE)) and were similar to salmon-derived carbon at -21.11±0.22 (n = 2). Rainbow trout collected in August were more depleted at 12.94±0.95(SE) $\partial^{15}N$ and -23.62±0.60(SE) $\partial^{13}C$ (n = 3).

An American dipper collected on Lower Troublesome Creek during spring 1988 was heavier isotopically (8.64 $\partial^{15}N$ versus 4.33 $\partial^{15}N$ and -23.74 $\partial^{13}C$ versus -33.33 $\partial^{13}C$) than two specimens collected during the same season from a control stream (Fish Creek, 62°50'N 152°45'W) geographically distant from any salmon streams (>50 km) though vegetationally similar to study streams. Two American dippers were collected on Lower Troublesome Creek during October 1988. The isotopic composition of one (8.30 $\partial^{15}N$/-26.49 $\partial^{13}C$) was similar to the bird collected in the spring on Troublesome Creek whereas the other bird was lighter (4.91 $\partial^{15}N$/-27.83 $\partial^{13}C$).

Figures 4.6a, 4.6b. Seasonal changes in isotope values for sculpin. Arrows indicate changes from April through Octorber of each year. Each sample is a composite of three similar-sized fish.1=April, 2=August, 3=October.





DISCUSSION

The mixing model put forward by Mathisen et al. (1988) provides a means of assessing significance of marine-derived nitrogen in a freshwater food web (Figure 4.7). The $\partial^{15}N$ and $\partial^{13}C$ values of major biota from my study streams, including primary food sources, are displayed in Figure 4.8. Riparian vegetation $\partial^{15}N$ and $\partial^{13}C$ values in my study are similar to other studies (Kline et al. 1989; Mook and Tan 1991) and showed no difference between enriched or control streams.

Values of $\partial^{15}N$ for adult salmon averaged 12.5‰ and were slightly heavier than the value of 11.2‰ reported by Klein et al (1989). The cause for this slightly enriched value is my inclusion of king salmon of higher trophic level (3-6 years at sea) in a composite value for four salmon species, whereas the Klein et al. (1989) value was for pink salmon (≥1 years at sea). Adult salmon reflect the trophic level and geographic region $\partial^{15}N$ and $\partial^{13}C$ values of where they fed. The larger fish in this study presumably fed on larger prey, hence the enriched value.

The $\partial^{15}N$ and $\partial^{13}C$ values of the macroinvertebrate community in Troublesome Creek were virtually the same at salmon-enriched and control sites in 1988 (Figure 4.3a), which was the only year salmon numbers were directly estimated. In contrast, values from 1990 show an average of 2‰ $\partial^{15}N$ enrichment in the salmon spawning section which translates, using the mixing model, into approximately 15% marine-derived nitrogen. High waters in 1989 and 1990 prevented estimates of salmon escapement, thus clear proof for a causal relationship between $\partial^{15}N$ enrichment and salmon numbers is lacking. Evidence for a potentially large salmon run in 1989 does exist (See Chapter 2). Casual field observations indicate rainbow trout (n = 6) collected

FIGURE 4.7. Mixing model modified from Mathisen et al. (1988). Light boxes indicate del 15 N of principal nitrogen sources. '✖' indicates % MDN of certain stream biota at their seasonal peaks.

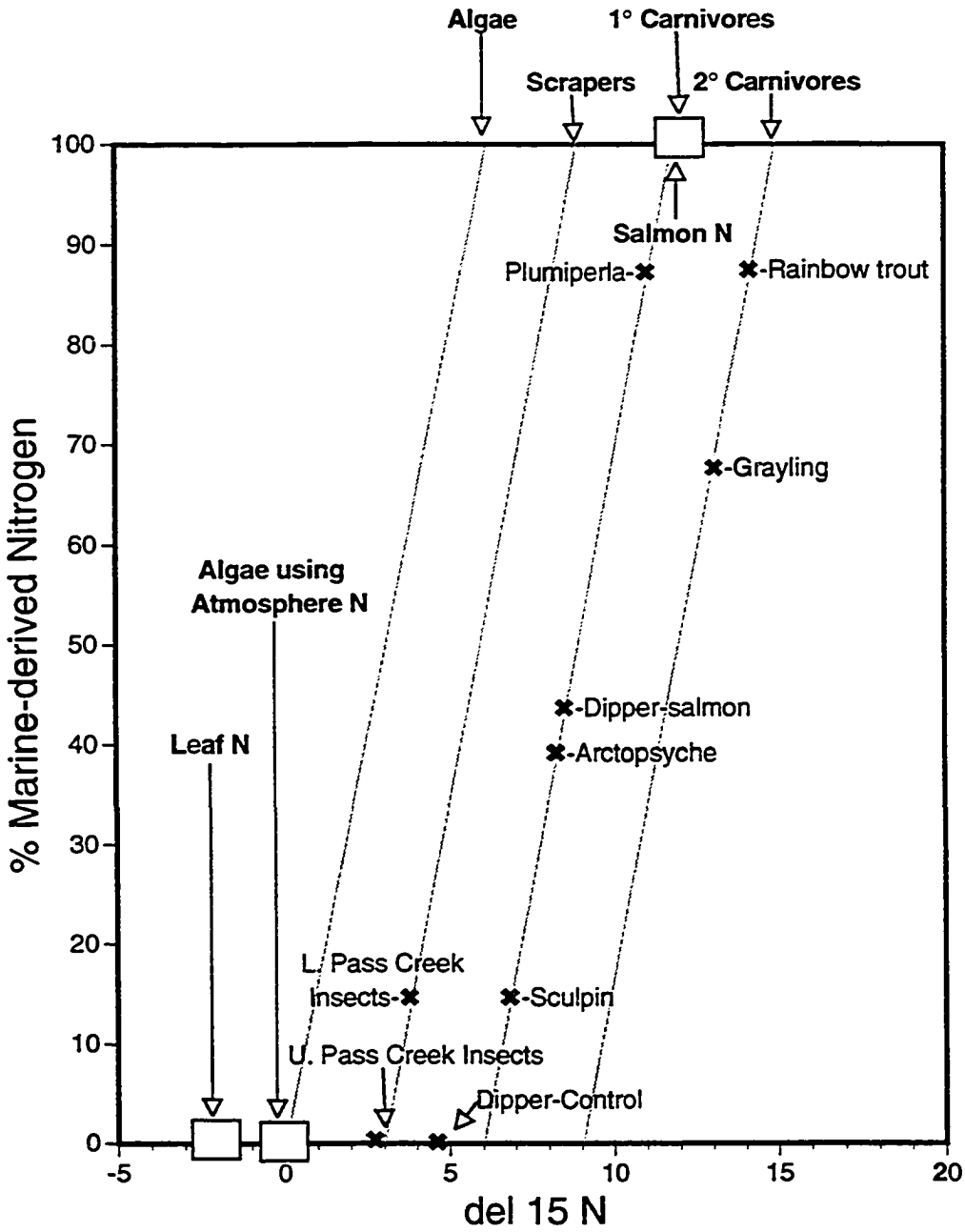
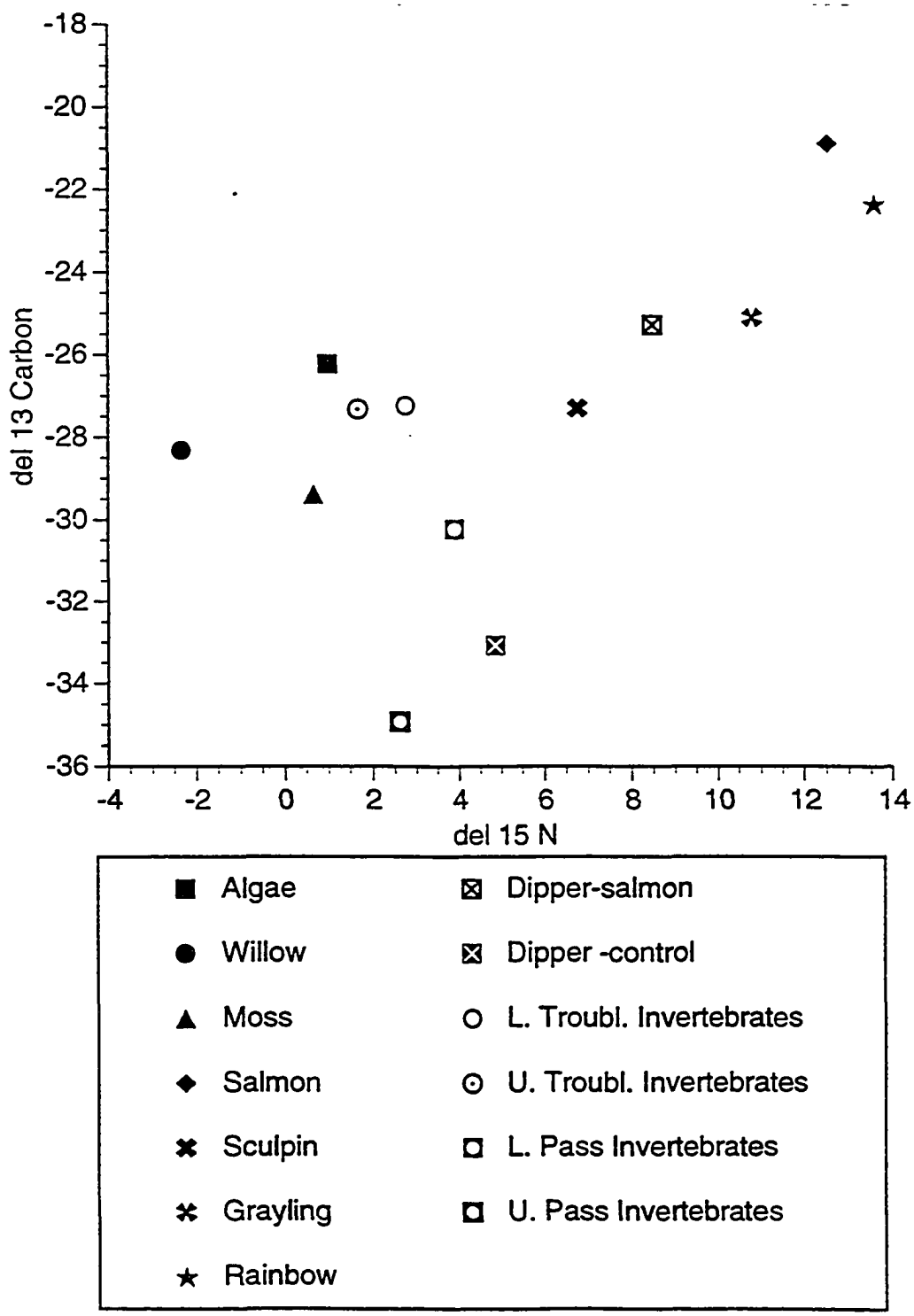


FIGURE 4.8. Average nitrogen and carbon isotope values for primary producers, macroinvertebrates and vertebrates from Troublesome and Pass Creeks, Alaska, in 1988 and 1990.



in June 1990 consumed far more (>2X) chum/pink smolts than rainbow trout had during June of both 1988 (n = 8) or 1989 (n = 5). The salmon run in Troublesome Creek in 1988 resulted in an estimated fertilization effect of ≈2 gm N/m^2 of streambed. Macroinvertebrate community isotopic evidence from 1990 suggests the 1989 run must have been greater than the 1988 run and was retained despite high discharge in 1989, consistent with studies that found that carcasses generally remain in spawning streams despite major floods (Glock et al. 1980; Cederholm et al. 1989).

Isotopic determinations of the macroinvertebrate community at salmon-enriched and control sites on Pass Creek shows an average 1‰ $\partial^{15}N$ enrichment in the salmon spawning section for 1988. The estimated run in 1988 resulted in a fertilization effect of ≈10 gm N/m^2 of streambed. A 2‰ $\partial^{15}N$ enrichment in the macroinvertebrate community in 1990 indicates larger runs in 1989-1990, but unfortunately without sustaining hard evidence. The 1988 and 1990 Pass Creek $\partial^{15}N$ values indicate slightly less <10% and about 15% marine-derived nitrogen, respectively. These estimates are based upon typical 3‰ enrichment per trophic level. While I did no lab experiments verifying enrichment of macroinvertebrates feeding on salmon, blowfly larvae in late instars taken from a carcass of a king salmon, (certainly close to 100% marine-derived nitrogen) showed less than a 1‰ enrichment in $\partial^{15}N$. If stream macroinvertebrates display similar fractionation with salmon, my estimates of the percentage of marine-derived nitrogen in the macroinvertebrate communities are conservative.

The cyclic seasonal pattern of isotope values seen for those few macroinvertebrate taxa consistently collected in both salmon enriched and

control sites parallels whole community isotope values. One mayfly genus (Ephemeroptera: Ephemerellidae: *Drunella*) was present at all sites at all times. This genus is both a scraper and predator, consuming the potentially marine-enriched biofilm on rocks along with large macroinvertebrates (including other predators). This 'generalist' approach to eating whatever is available in the greatest quantities resulted in the isotope values for *Drunella* being the best general indicator of system enrichment by salmon. Overall, predators (Plecoptera: Perlodidae-*Isoperla*) and filter-feeders (Trichoptera: Hydropsychidae-*Arctopsyche;* Diptera: Simuliidae-*Prosimulium*) tracked enrichment well. Obligate shredders such as craneflies Diptera: Tipulidae-*Tipula*) and winter stoneflies (Plecoptera: Nemouridae-*Zapada*), which focus on leaf tissue as their food source are poor indicators of system enrichment by salmon. Although annual values of $\partial^{15}N$ for the macroinvertebrate community as a whole did not show a high percentage of marine-derived nitrogen, one less-common taxon did show a large salmon enrichment effect. The value of one predatory stonefly (Plecoptera: Chloroperlidae-*Plumiperla*), was 10.2‰ for June 1990 reflecting 90% marine-derived nitrogen .

Sculpin were the only fish collected at both salmon enriched and control sites on both creeks. The most notable feature in these data are a lack of significant seasonal variation at all sites compared to the data for macroinvertebrates. Their $\partial^{15}N$ values trend slightly heavier throughout the ice-free season failing to shadow that of the macroinvertebrate community. Likewise, $\partial^{13}C$ values of sculpins stay nearly the same or trend heavier seasonally again contrasting with that of the macroinvertebrate community.

This outcome may be a function of slow turnover of carbon and nitrogen in sculpin tissue (Fry and Arnold 1982; Rosenfeld and Rolf 1992) or a specific and unchanging food choice. During the observed heavy salmon run on Lower Pass Creek in 1988, the apparent heavy salmon run on Lower Troublesome Creek in 1989, $\partial^{13}C$ values in sculpin changed only slightly, while $\partial^{15}N$ values increased. Because a similar enrichment did not occur in control sections of respective streams, this change indicates the addition of salmon-derived nitrogen to stream food webs through 1° producers. There was no increase in $\partial^{13}C$ values which would have occurred with direct ingestion of salmon tissue. An interior Alaska study reported little sign of sculpins eating salmon eggs although salmon were present in low numbers at the site (Sonnichsen 1981). Using isotope values of fish from salmon-free areas as indicating 0% marine-derived, most $\partial^{15}N$ values for sculpins usually represented 0% marine-derived nitrogen except for Lower Pass Creek 1988 when it approached 30%.

Grayling were only collected at Lower Pass Creek in 1990. Their $\partial^{13}C$ isotope values represent an enrichment of ≈6‰ compared to their potential food, the salmon-enriched macroinvertebrate community in Lower Pass Creek. Given an average enrichment of 1‰ per trophic level (Fry and Sherr 1984), grayling could not display such enrichment from eating stream insects. A diet of predominately terrestrial insects, unlikely at -28‰, would still leave an enrichment of 2‰ unaccounted for. The $\partial^{15}N$ value of ≈11‰ for grayling could not come from a diet dominated by invertebrates eating terrestrial leaves, which probably averages 1‰ (leaves ≈ -2.0‰ + 3‰ trophic enrichment (DeNiro and Epstein 1978)). A typical enrichment of 3‰ would give the grayling a value of 4‰. Therefore, grayling must have directly

ingested substantial amounts of salmon tissue in Lower Pass Creek in 1990. This is supported by seasonal carbon and nitrogen-isotope values for grayling that became more enriched over the course of the spawning period for salmon. Grayling $\partial^{15}N$ values reflect approximately 60% marine-derived nitrogen.

Values of $\partial^{15}N$ and $\partial^{13}C$ for rainbow trout reflects a diet similar to that of grayling, but probably with more salmon in their diet given the rainbows' more enriched values. Spring and Autumn samples are both very enriched compared to their respective stream macroinvertebrate community and are similar to those reported by Kline et al. (1989). These values reflect approximately 85% marine-derived nitrogen.

Values of $\partial^{15}N$ and $\partial^{13}C$ for coho fry during their first summer of life lighten slightly by July but become enriched by October nearly matching their values at emergence and those of adult grayling. Clearly, the diet of salmon fry during salmon spawning must largely consist of flesh of adult salmon rather than less-enriched macroinvertebrates.

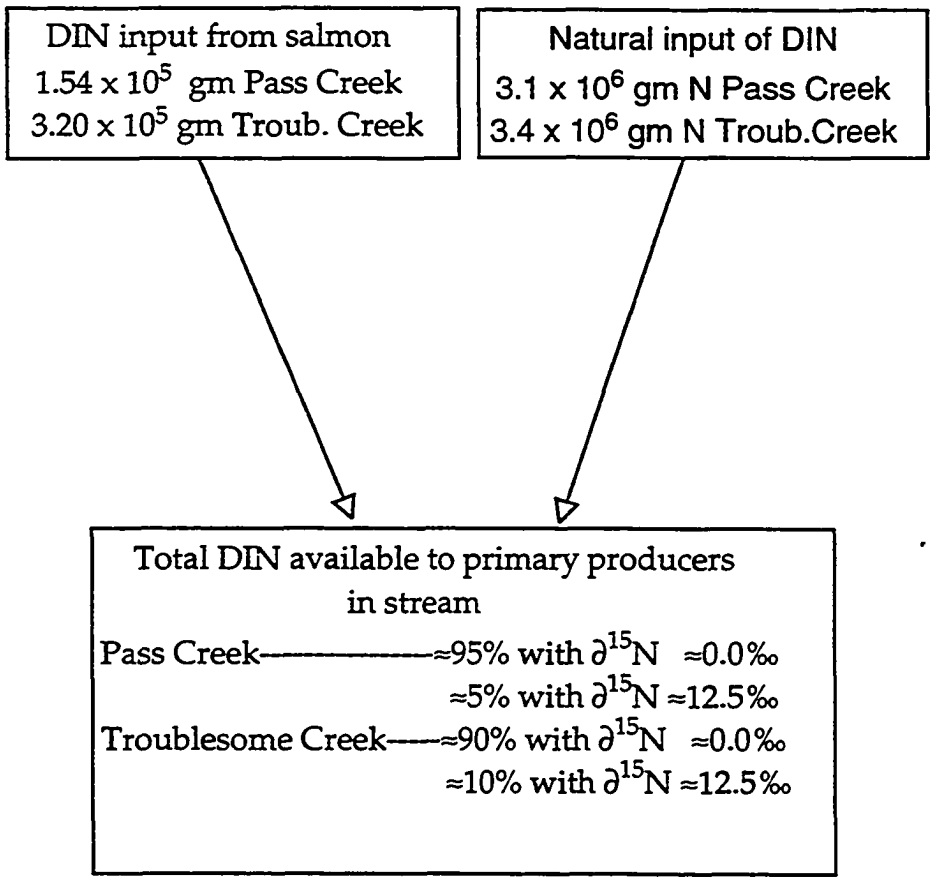
The stable-isotope values for an American dipper collected from an unfrozen stretch of Lower Troublesome Creek in early May were more than twice what would be expected from the stream macroinvertebrate values adjusted for isotopic enrichment (typically +1 $\partial^{13}C$, +3 $\partial^{15}N$). This bird probably fed on salmon biomass. This supports observations by me and others that dippers eat both salmon flesh and salmon eggs (Cederholm et al. 1989). Two dippers collected from the unfrozen open stretches of a control stream (no salmon) in April displayed a depleted isotopic composition contrasting strongly with the Lower Troublesome Creek bird, but showing appropriate

enrichment from macroinvertebrates at that unenriched location. This supports other studies showing dominance in dipper diets of stream insects (Ehrlich et al. 1988). Two birds collected during October 1988 at Lower Troublesome Creek had strikingly different isotope values. One bird was similar to those birds collected at that location in May; the other bird, being lighter, nearly matching the isotopic composition of a bird collected from the control stream the previous spring. I speculate the latter was a transient from an unenriched system making a typically long migration from higher altitude summer range, to lower altitude winter range (Lundberg et al. 1981). This highlights the importance of sampling particular biota at a time appropriate to collecting residents rather than transients. In sum, these measurements are further evidence of movement of salmon-derived nitrogen through stream food webs to higher trophic levels.

My stable-isotope data for leaves, algae, salmon, and rainbow trout is similar to those reported by Kline et al. (1989). Their estimates of marine-derived nitrogen in stream food webs are higher, probably because of two variables future researchers should consider. Sashin Creek received a much larger run of salmon (>2X to 3X) utilizing a smaller spawning area, and I speculate, the total dissolved nitrogen (TDN) content of that creek water may have been lower given the copious precipitation in that region. Although spawning activities of thousands of salmon in my study streams is certainly impressive, the amount of marine-derived nitrogen available to stream food webs may actually be small compared to the yearly amount of TDN naturally occurring in even nutrient-poor streams.

Using a series of assumptions applicable to the watershed, a conceptual

Figure 4.9. Conceptual model of dissolved inorganic nitrogen (DIN) inputs into Pass Creek and Troublesome Creek.



Assumptions:

1-all salmon nitrogen loading is at upstream end and at a consistent rate over the input interval

2-the input interval is 90 days (July through September)

3-all salmon decompose in place

4-DON input/loss is low relative to DIN production

5-uptake by plants of DON<<DIN

model can be constructed (Figure 4.9). The assumptions of this model are: 1) all salmon nitrogen loading is at the upstream end and at a consistent rate over the input interval; 2) the input interval is 90 days (July through September); 3) all salmon decompose in place; 4) dissolved organic nitrogen (DON) input/loss is low relative to dissolved inorganic nitrogen (DIN) production; and 5) uptake by plants of DON<<DIN. Using a typical oligotrophic stream water concentration of 200 mg DIN·m^{-3} (Wetzel 1983) and the measured average discharge for the study streams, the estimated amount of TDN naturally available to stream primary producers and microbiota is 3.1 x 10^6 gm for Pass Creek (0.2 gm/m^3 TDN·2.0 m^3/sec·60 sec.·60 min.·24 hours·90 days) and is 3.4 x 10^6 gm for Troublesome Creek (0.2 gm/m^3 TDN·2.5 m^3/sec·60 sec.·60 min.·24 hours·90 days) for the 90-day spawning period. This contrasts with previously calculated 1988 inputs from salmon of 1.54 x 10^5 gm and 3.2 x 10^5 gm of nitrogen, respectively. Natural levels of TDN, present in 10 to 20 times the quantity brought into the stream by salmon, should and did reduce the marine signal in most stream biota to <10% marine-derived nitrogen, except for those biota keyed into direct consumption of salmon. Similarly, Rand et al. (1992) found that several streams flowing into Lake Ontario were so naturally rich in nutrients that inputs from decomposing salmon could not substantially increase primary productivity because the systems were already light limited.

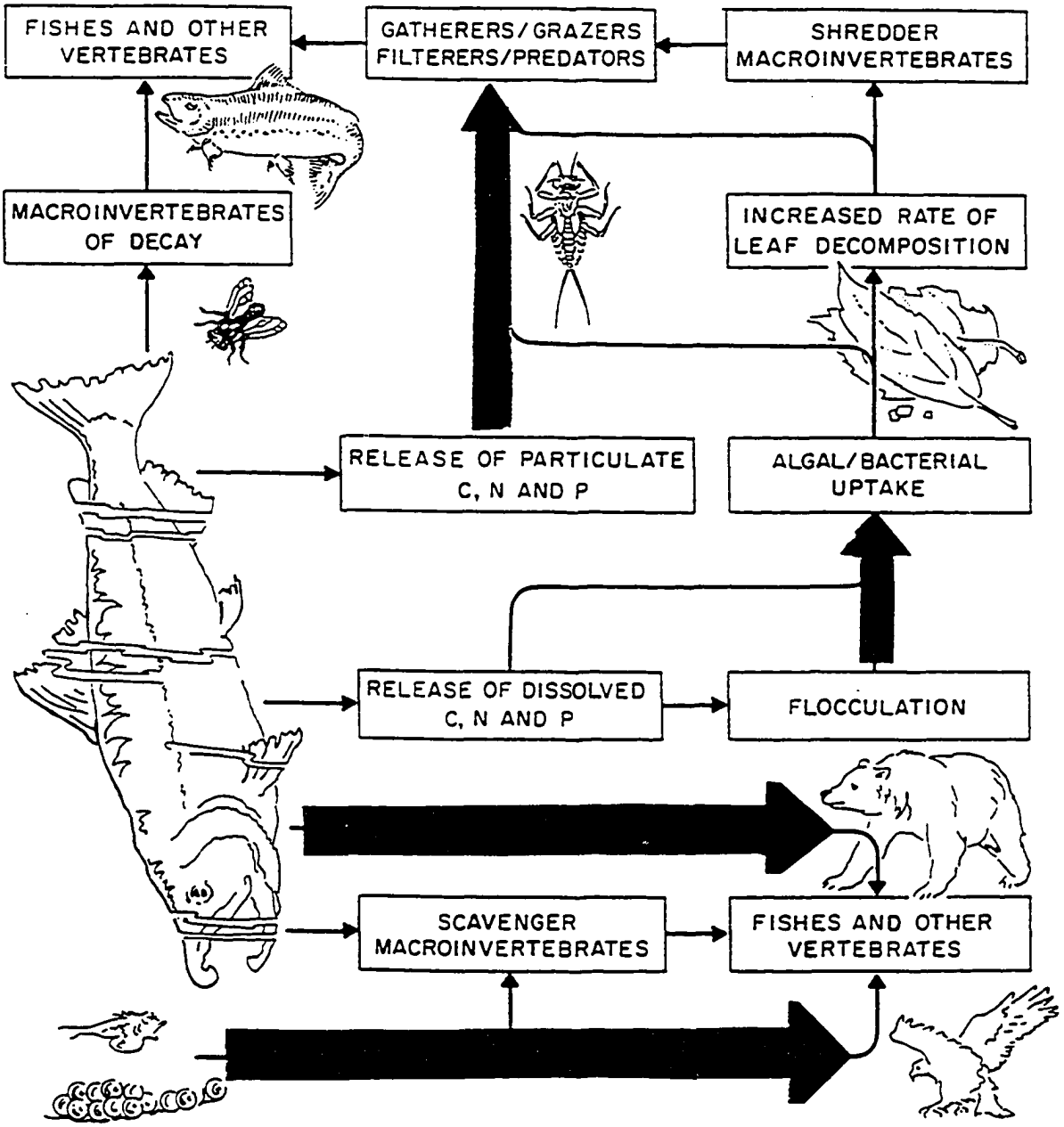
My study shows that marine-derived nitrogen from salmon runs adds to the total available nitrogen pool and is used by the biota in oligotrophic streams. Secondary productivity in the macroinvertebrate community may increase from this added nitrogen, either through stimulation of algal

production (and increased food availability to consumers) or, more likely, direct ingestion of salmon tissue. In turn, greater secondary production of macroinvertebrates should result in greater production of salmon fry and resident fish.

The high percent of marine-derived nitrogen in stream fish from salmon fry and sculpin to grayling and rainbow trout is a truly exciting finding. This outcome suggests that marine-derived nitrogen and marine-derived carbon get into stream fish through direct consumption of salmon biomass rather than through food webs (ie. uptake of marine-derived nitrogen by biofilm or leaf litter eaten by macroinvertebrates eaten by fish). Fertilization, as now done for some red salmon nursery lakes, may do little to increase resident fish and populations of rearing salmon fry when these fish actually depend upon salmon biomass. Salmon tissue, be it eggs, flesh, or fry, may be the key component in maintaining fish-rich streams in an otherwise nutrient-poor subarctic environment. The magnitude of the potential effects (figure 1.1) of salmon carcasses on spawning stream biota is repicted in Figure 4.10.

In contrast to nitrogen, isotopic evidence for the contribution of marine-derived carbon to food webs in streams is not clear. Marine carbon is difficult to differentiate from nonmarine carbon because the $\partial^{13}C$ value of freshwater primary producers varies widely depending upon the source of derived $C0_2$ (Peterson and Fry 1987). In this vein, the waterfalls on the streams probably alter dissolved inorganic carbon values considerably from groundwater inputs for an unknown distance below the waterfall. I noted extensive use of salmon carcasses by virtually all stream macroinvertebrates,

FIGURE 4.10. Conceptual diagram of actual effects of salmon carcasses on spawning streams.



but the carbon composition of the macroinvertebrate community, when taken as a whole, did not show substantial marine derivation to benthic consumers. Still, salmon flesh may be very important to benthic consumers. A high-quality diet, (low C:N ratio), may facilitate, if not actually be required for, the transition from the larval or nymphal phase of macroinvertebrates to that of adult (Anderson and Cummins 1979). Further studies might investigate whether stream insects from enriched areas display earlier times of emergence than in control areas. Adult stages of aquatic insects from salmon-enriched areas could display a marine carbon signal, whereas aquatic, immature stages, composed of many individuals that may not survive to emergence, do not. Adult macroinvertebrates from systems enriched by salmon may also be larger, display greater Darwinian fitness and be important in colonizing and maintaining robust macroinvertebrate communities in nearby nonsalmon streams.

Salmon carcasses do play a role in maintaining biotic diversity and enhancing production in Alaskan streams and associated watersheds. Predatory macroinvertebrates and stream fishes consistently show a surprisingly strong marine-derived nitrogen signal. This connection of salmon carcasses, eggs, and fry to scavenger and predatory macroinvertebrates and fish may be a key linkage in sustained productivity of salmon streams. Studies so far have been short term and without applied phases. Potentially cumulative effects of run failures are unknown. The cultural and economic importance of salmon in Alaska and throughout the Pacific Northwest demands we learn more.

Chapter 5- Summary and Future Directions

The results of all three elements of this investigation support the hypothesis that salmon (*Oncorhynchus* spp.) carcasses can be an important contribution to the energetics of the aquatic communities of southcentral Alaska streams that receive salmon runs. The process of salmon carcass decomposition is described, along with decomposition rates for unspawned carcasses in salmon spawning streams. Lotic macroinvertebrate community structure was affected by salmon carcass-induced stream enrichment. stable-isotope studies showed that marine-derived nitrogen enters stream food webs, becoming important for certain aquatic biota. My findings are summarized in the following statements:

Abiotic mechanisms aid retention of salmon carcasses in streams.

- Shallow, slow-moving waters that salmon seek before death aids stream retention of carcasses after fish death.
- Large debris in streams, especially boulders, root wads and branches, effectively catch and hold drifting carcasses, retarding further downstream movement.
- Carcasses, usually negatively buoyant, are readily trapped in the turbulence behind large instream objects. Once detained, they are often covered with sand and gravel, becoming part of the benthos.
- Decomposing carcasses caught in strong current are subject to moderate turbulence and abrasion against bottom structures resulting in further carcass disintegration. Partially decomposed carcasses often come apart in stream turbulence. Fragments settle into the boundary layer, becoming more available for macroinvertebrate use and

are no longer subject to downstream movement.

There are biotic mechanisms for retaining salmon carcasses in streams.

- Salmon, abraded by spawning activities, often display extensive fungal infections when alive, likely facilitating rapid decay after death.
- The sewage fungus complex likely provides a sink and reservoir for salmon carbon and nutrients.
- Stream macroinvertebrates rapidly colonize exposed tissue of carcasses and can, under appropriate conditions, contribute significantly to carcass disintegration.
- Sculpin, king and silver salmon fry, rainbow trout and grayling all eat salmon biomass. Casual observations from this study suggest salmon fry may play a role in carcass disintegration.

The macroinvertebrate community in streams receiving salmon runs changes in response to enrichment.

- Filter-feeders, including rare to Alaska net-spinning caddis flies, generally increase with enrichment.
- Taxa richness and diversity increase in response to enrichment from salmon and lake outlet seston.
- Many individual taxa display a response (either positive or negative) to enrichment as evidenced by differences in individual weight or proportional representation in community biomass.
- Complexity of the macroinvertebrate community increased in spawning streams that have lakes as sources.

A significant difference in $\partial^{15}N$ values exists between marine-derived nitrogen (the five species of Pacific salmon) and both aquatic and terrestrial food sources.

- Adult anadromous salmon had a combined $\partial^{15}N$ value of ≈12.5‰.
- Terrestrial vegetation had a combined $\partial^{15}N$ value of ≈-2.0‰.
- Aquatic algae displayed a $\partial^{15}N$ value range of ≈1.0‰

Natural dissolved inorganic nitrogen contributions from groundwater to stream food webs was larger than marine input.

- Calculations of natural inputs of dissolved inorganic nitrogen over the course of the spawning period were 10X to 20X greater than the maximum potential available from salmon carcasses.
- $\partial^{15}N$ values for aquatic primary producers and the aquatic macroinvertebrate community taken from enriched areas reflected a slight, but proportionate (<5% to 10%), enrichment over control areas.

$\partial^{15}N$ levels in stream biota ranged considerably.

- $\partial^{15}N$ values for certain stream insect taxa, salmon fry, grayling and rainbow trout from salmon enriched streams suggests salmon protein is their predominant food. Two peaks were observed: after chum and pink salmon fry outmigration in early summer and after salmon spawning activities in the fall.
- $\partial^{15}N$ values for most macroinvertebrate taxa and sculpin suggest marine-derived nitrogen enters food webs after its incorporation into algal biomass rather than direct consumption.
- $\partial^{15}N$ values for several American dippers were enriched when compared to macroinvertebrate community values at their apparent feeding location. $\partial^{15}N$ values of a bird from a salmon spawning stream suggested it had consumed significant amount of salmon biomass.
- $\partial^{15}N$ values in individual macroinvertebrate taxa usually cycled seasonally.

$\partial^{13}C$ values in stream biota ranged considerably.

- $\partial^{13}C$ values for algal samples varied significantly spatially and temporally. Such measurements are crude given the complexity of any algal community. Whether such gross measurements reflect what is consumed and assimilated by macroinvertebrates is unclear.
- Extremely low values (-45‰) for macroinvertebrates collected from some systems in April suggests respired carbon can become an increasingly large component of the dissolved organic carbon pool in groundwater by the end of winter.

The findings described in this thesis have potential for further application and research.

The composition and dynamics of stream macroinvertebrate communities in Alaska are inadequately understood.

- A comprehensive monitoring program should be established for each bioregion (Oswood 1989) establishing baseline data for important systems.
- The role of lake outlet streams in maintaining diverse macroinvertebrate communities needs further investigation.

Typical macroinvertebrate sampling techniques should be reassessed as to their reliability in assessing community structure.

- Macroinvertebrate semi-quantitative sampling, as described here, and the use of biomass, rather than density, should be compared to traditional Surber sampling.

stable-isotope techniques will work well for assessing the importance of marine-derived nitrogen to food webs in salmon-spawning streams.

- $\partial^{15}N$ fractionation values for aquatic macroinvertebrates feeding on salmon should be determined to better assess salmon carcass importance in stream food webs. $\partial^{15}N$ fractionation value for blowfly larva feeding on salmon was only one-third of the expected increase (Minigawa and Wada 1984).
- Targeting only certain biota (enrichment indicator organisms) will save collection time and sample preparation costs. These biota are predator stream insects, rearing salmon fry, grayling and rainbow trout.
- Denitrification appears to occur on at least one southcentral Alaska stream. The downstream effect from suspected locales, (beaver ponds,

sloughs and small bodies of water), on $\partial^{15}N$ and $\partial^{13}C$ values should be investigated.

- The carbon-isotope picture presented here is unclear probably because of differences in values for source dissolved inorganic carbon (DIC). Comparisons between systems is often questionable (Kling and Fry 1992). Regular $\partial^{13}C$ measurements of DIC in stream water may clarify variable algal $\partial^{13}C$ values.

Artificial fertilization of salmon streams to restore salmon fry and sport fish production should be explored using separate treatments of salmon carcasses and artificial fertilizers.

- Carcasses appear to enter food webs differently in streams versus lakes. Different applications with aforementioned supplements will clarify this hypothesis.

Anadromous fish may function as keystone food resource for both aquatic and terrestrial biota.

- Salmon runs have a recognized but unquantified effect on terrestrial biota (Cederholm et al. 1989; Wilson and Halupka in press). The potential for cascading trophic interactions (Carpenter et al. 1985) requires a whole system, rather than narrow, research approach.
- Casual observations from this study specifically suggest American dipper, merganser, and harlequin duck numbers in a system may reflect past salmon escapements.
- Surveys of major biota (ie. bears, mustelids, birds) in both salmon-enriched and control streams will allow an integrated view of whole system interactions.

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APPENDIX A-Community Macroinvertebrate Data

	A	B	C	D	E	F
1			COLLECTOR-GATHERERS			
2	Date/Stream/Year	Code	Ameletus	Baetis	Ephemerella	Psychoglypha
3	Byers-April-1988	#	1	37	24	
4		%Total#	0.45%	16.59%	10.76%	
5		wt mg	1	10	75	
6		%Total dry wt.	0.38%	3.83%	28.74%	
7		wt/invert	1.00	0.27	3.13	
8	Byers-June-1988	#		245	85	23
9		%Total#		13.11%	4.55%	1.23%
10		wt mg		64	169	47
11		%Total dry wt.		14.22%	37.56%	10.44%
12		wt/invert		0.26	1.99	2.04
13	Byers-August-1988	#	4	104	165	7
14		%Total#	0.19%	5.03%	7.98%	0.34%
15		wt mg	1	14	26	99
16		%Total dry wt.	0.20%	2.85%	5.30%	20.16%
17		wt/invert	0.25	0.13	0.16	14.14
18	Byers-October-1988	#		44	478	
19		%Total#		2.80%	30.45%	
20		wt mg		1	459	
21		%Total dry wt.		0.11%	51.00%	
22		wt/invert		0.02	0.96	
23	Honolulu-April-1988	#	34	477		
24		%Total#	3.24%	45.47%		
25		wt mg	44	202		
26		%Total dry wt.	9.17%	42.08%		
27		wt/invert	1.29	0.42		
28	Honolulu-June-1988	#	22	563		
29		%Total#	0.60%	15.41%		
30		wt mg	9	132		
31		%Total dry wt.	2.00%	29.33%		
32		wt/invert	0.41	0.23		
33	Honolulu-August-1988	#	2	10		
34		%Total#	0.11%	0.55%		
35		wt mg	2	18		
36		%Total dry wt.	0.63%	5.66%		
37		wt/invert	1.00	1.80		
38	Honolulu-October-1988	#	19	24		
39		%Total#	2.38%	3.01%		
40		wt mg	17	3		
41		%Total dry wt.	5.70%	1.01%		
42		wt/invert	0.89	0.13		
43	L. Pass-April-1988	#		38	32	
44		%Total#		18.63%	15.69%	
45		wt mg		8	579	
46		%Total dry wt.		0.71%	51.38%	
47		wt/invert		0.21	18.09	
48	L. Pass-June-1988	#	27	44	45	72
49		%Total#	2.91%	4.74%	4.84%	7.75%
50		wt mg	22	1	14	9
51		%Total dry wt.	2.86%	0.13%	1.82%	1.17%
52		wt/invert	0.81	0.02	0.31	0.13
53	L. Pass-August-1988	#	6	63	271	99
54		%Total#	0.32%	3.33%	14.32%	5.23%
55		wt mg	1	16	18	276
56		%Total dry wt.	0.15%	2.34%	2.63%	40.29%
57		wt/invert	0.17	0.25	0.07	2.79
58	L. Pass-October-1988	#			34	
59		%Total#			10.12%	
60		wt mg			12	
61		%Total dry wt.			4.76%	
62		wt/invert			0.35	
63	L.Troublesome-April-1988	#	21	218	111	12
64		%Total#	3.25%	33.75%	17.18%	1.86%
65		wt mg	1	138	199	1
66		%Total dry wt.	0.12%	16.87%	24.33%	0.12%
67		wt./invert	0.05	0.63	1.79	0.08

	A	B	C	D	E	F
68	L.Troublesome-June-1988	#	3	347	30	174
69		%Total#	0.16%	17.93%	1.55%	8.99%
70		wt mg	1	48	107	7
71		%Total dry wt.	0.17%	8.12%	18.10%	1.18%
72		wt./invert	0.33	0.14	3.57	0.04
73	L.Troublesome-August-1988	#	7	178	127	136
74		%Total#	0.27%	6.95%	4.96%	5.31%
75		wt mg	1	12	1	117
76		%Total dry wt.	0.19%	2.23%	0.19%	21.71%
77		wt./invert	0.14	0.07	0.01	0.86
78	L.Troublesome-October-1988	#		14	95	
79		%Total#		1.91%	12.94%	
80		wt mg		1	47	
81		%Total dry wt.		0.17%	7.83%	
82		wt./invert		0.07	0.49	
83	U. Pass-April-1988	#		24	133	
84		%Total#		9.56%	52.99%	
85		wt mg		4	204	
86		%Total dry wt.		0.88%	45.03%	
87		wt./invert		0.17	1.53	
88	U. Pass-June-1988	#		98	90	139
89		%Total#		11.89%	10.92%	16.87%
90		wt mg		25	465	15
91		%Total dry wt.		4.33%	80.45%	2.60%
92		wt./invert		0.26	5.17	0.11
93	U. Pass-August-1988	#		1	195	139
94		%Total#		0.11%	20.68%	14.74%
95		wt mg		1	35	264
96		%Total dry wt.		0.21%	7.28%	54.89%
97		wt./invert		1.00	0.18	1.90
98	U. Pass-October-1988	#			251	11
99		%Total#			24.54%	1.08%
100		wt mg			81	41
101		%Total dry wt.			22.07%	11.17%
102		wt./invert			0.32	3.73
103	U.Troublesome-April-1988	#	16	30	11	
104		%Total#	9.70%	18.18%	6.67%	
105		wt mg	7	3	21	
106		%Total dry wt.	4.43%	1.90%	13.29%	
107		wt./invert	0.44	0.10	1.91	
108	U.Troublesome-June-1988	#		84	17	69
109		%Total#		6.02%	1.22%	4.95%
110		wt mg		13	44	54
111		%Total dry wt.		2.47%	8.35%	10.25%
112		wt./invert		0.15	2.59	0.78
113	U.Troublesome-August-1988	#		10	39	9
114		%Total#		2.46%	9.58%	2.21%
115		wt mg		3	4	50
116		%Total dry wt.		1.73%	2.31%	28.90%
117		wt./invert		0.30	0.10	5.56
118	U.Troublesome-October-1988	#			60	1
119		%Total#			10.85%	0.18%
120		wt mg			8	5
121		%Total dry wt.			2.89%	1.81%
122		wt./invert			0.13	5.00

	G	H	I	J	K	L	M
1						SCRAPERS	
2	Pericoma	Chironomidae	Oligochaete	Turbellaria	Nematoda	Heptageniidae	Glossasoma
3		10				18	
4		4.48%				8.07%	
5		1				12	
6		0.38%				4.60%	
7		0.10				0.67	
8		485	11	50	1	171	251
9		25.95%	0.59%	2.68%	0.05%	9.15%	13.43%
10		19	1	1	1	19	14
11		4.22%	0.22%	0.22%	0.22%	4.22%	3.11%
12		0.04	0.09	0.02	1.00	0.11	0.06
13	10	440			2	115	340
14	0.48%	21.28%			0.10%	5.56%	16.44%
15	99	13			1	17	17
16	20.16%	2.65%			0.20%	3.46%	3.46%
17	9.90	0.03			0.50	0.15	0.05
18	10	138	13			73	78
19	0.64%	8.79%	0.83%			4.65%	4.97%
20	8	23	53			8	42
21	0.89%	2.56%	5.89%			0.89%	4.67%
22	0.80	0.17	4.08			0.11	0.54
23		51				141	
24		4.86%				13.44%	
25		10				109	
26		2.08%				22.71%	
27		0.20				0.77	
28		456		100		2295	2
29		12.48%		2.74%		62.83%	0.05%
30		40		8		133	1
31		8.89%		1.78%		29.56%	0.22%
32		0.09		0.08		0.06	0.50
33		22				1447	15
34		1.20%				79.03%	0.82%
35		8				223	3
36		2.52%				70.13%	0.94%
37		0.36				0.15	0.20
38		285				276	15
39		35.71%				34.59%	1.88%
40		42				107	3
41		14.09%				35.91%	1.01%
42		0.15				0.39	0.20
43		16				5	
44		7.84%				2.45%	
45		18				25	
46		1.60%				2.22%	
47		1.13				5.00	
48		199				108	1
49		21.42%				11.63%	0.11%
50		54				28	1
51		7.01%				3.64%	0.13%
52		0.27				0.26	1.00
53		376			1	114	121
54		19.87%			0.05%	6.03%	6.40%
55		100			1	16	33
56		14.60%			0.15%	2.34%	4.82%
57		0.27			1.00	0.14	0.27
58		26				6	129
59		7.74%				1.79%	38.39%
60		16				1	6
61		6.35%				0.40%	2.38%
62		0.62				0.17	0.05
63		50				35	
64		7.74%				5.42%	
65		3				16	
66		0.37%				1.96%	
67		0.06				0.46	

	G	H	I	J	K	L	M
68		492				351	
69		25.43%				18.14%	
70		26				64	
71		4.40%				10.83%	
72		0.05				0.18	
73		293				448	192
74		11.44%				17.49%	7.49%
75		26				81	10
76		4.82%				15.03%	1.86%
77		0.09				0.18	0.05
78		54				108	32
79		7.36%				14.71%	4.36%
80		6				56	1
81		1.00%				9.33%	0.17%
82		0.11				0.52	0.03
83						13	
84						5.18%	
85						51	
86						11.26%	
87						3.92	
88		104			2	94	37
89		12.62%			0.24%	11.41%	4.49%
90		12			1	32	2
91		2.08%			0.17%	5.54%	0.35%
92		0.12			0.50	0.34	0.05
93	3	61				30	48
94	0.32%	6.47%				3.18%	5.09%
95	1	5				25	1
96	0.21%	1.04%				5.20%	0.21%
97	0.33	0.08				0.83	0.02
98		294				74	63
99		28.74%				7.23%	6.16%
100		14				16	18
101		3.81%				4.36%	4.90%
102		0.05				0.22	0.29
103		10				40	
104		6.06%				24.24%	
105		3				10	
106		1.90%				6.33%	
107		0.30				0.25	
108		135				189	1
109		9.68%				13.55%	0.07%
110		10				68	1
111		1.90%				12.90%	0.19%
112		0.07				0.36	1.00
113		59				59	17
114		14.50%				14.50%	4.18%
115		7				10	1
116		4.05%				5.78%	0.58%
117		0.12				0.17	0.06
118		21				40	37
119		3.80%				7.23%	6.69%
120		1				8	2
121		0.36%				2.89%	0.72%
122		0.05				0.20	0.05

	N	O	P	Q	R	S	T
1			PREDATORS				
2	Apatania	Gastropoda	Drunella	Isoperla	Plumiperla	Rhyacophila	Empididae
3			19		14		
4			8.52%		6.28%		
5			41		24		
6			15.71%		9.20%		
7			2.16		1.71		
8			30	9	18		2
9			1.61%	0.48%	0.96%		0.11%
10			56	2	2		1
11			12.44%	0.44%	0.44%		0.22%
12			1.87	0.22	0.11		0.50
13	87	1	196	11	27	1	28
14	4.21%	0.05%	9.48%	0.53%	1.31%	0.05%	1.35%
15	3	1	4	3	3	1	2
16	0.61%	0.20%	0.81%	0.61%	0.61%	0.20%	0.41%
17	0.03	1.00	0.02	0.27	0.11	1.00	0.07
18	64		98	31	4		17
19	4.08%		6.24%	1.97%	0.25%		1.08%
20	42		7	23	1		4
21	4.67%		0.78%	2.56%	0.11%		0.44%
22	0.66		0.07	0.74	0.25		0.24
23				9	40		
24				0.86%	3.81%		
25				14	49		
26				2.92%	10.21%		
27				1.56	1.23		
28			3	10	67	3	
29			0.08%	0.27%	1.83%	0.08%	
30			9	13	9	1	
31			2.00%	2.89%	2.00%	0.22%	
32			3.00	1.30	0.13	0.33	
33			17		76	2	3
34			0.93%		4.15%	0.11%	0.16%
35			4		29	1	1
36			1.26%		9.12%	0.31%	0.31%
37			0.24		0.38	0.50	0.33
38			6	7	18	1	
39			0.75%	0.88%	2.26%	0.13%	
40			4	32	2	1	
41			1.34%	10.74%	0.67%	0.34%	
42			0.67	4.57	0.11	1.00	
43			28	5			
44			13.73%	2.45%			
45			125	25			
46			11.09%	2.22%			
47			4.46	5.00			
48		1	107	8	58	7	4
49		0.11%	11.52%	0.86%	6.24%	0.75%	0.43%
50		1	524	5	64	1	1
51		0.13%	68.05%	0.65%	8.31%	0.13%	0.13%
52		1.00	4.90	0.63	1.10	0.14	0.25
53	18	1	377	37	4	7	3
54	0.95%	0.05%	19.93%	1.96%	0.21%	0.37%	0.16%
55	1	1	105	3	3	3	1
56	0.15%	0.15%	15.33%	0.44%	0.44%	0.44%	0.15%
57	0.06	1.00	0.28	0.08	0.75	0.43	0.33
58	21		39	7	1	3	5
59	6.25%		11.61%	2.08%	0.30%	0.89%	1.49%
60	11		7	1	2	1	1
61	4.37%		2.78%	0.40%	0.79%	0.40%	0.40%
62	0.52		0.18	0.14	2.00	0.33	0.20
63			49	2	8	22	
64			7.59%	0.31%	1.24%	3.41%	
65			120	21	13	80	
66			14.67%	2.57%	1.59%	9.78%	
67			2.45	10.50	1.63	3.64	

	N	O	P	Q	R	S	T
68			79	1	106	14	
69			4.08%	0.05%	5.48%	0.72%	
70			238	1	21	3	
71			40.27%	0.17%	3.55%	0.51%	
72			3.01	1.00	0.20	0.21	
73	6		632	3	129	17	7
74	0.23%		24.67%	0.12%	5.04%	0.66%	0.27%
75	1		161	1	39	5	1
76	0.19%		29.87%	0.19%	7.24%	0.93%	0.19%
77	0.17		0.25	0.33	0.30	0.29	0.14
78			145	19	4	34	7
79			19.75%	2.59%	0.54%	4.63%	0.95%
80			116	11	2	10	1
81			19.33%	1.83%	0.33%	1.67%	0.17%
82			0.80	0.58	0.50	0.29	0.14
83			3	8	2		
84			1.20%	3.19%	0.80%		
85			5	9	2		
86			1.10%	1.99%	0.44%		
87			1.67	1.13	1.00		
88			5	5	3		3
89			0.61%	0.61%	0.36%		0.36%
90			2	2	2		1
91			0.35%	0.35%	0.35%		0.17%
92			0.40	0.40	0.67		0.33
93	45		70				1
94	4.77%		7.42%				0.11%
95	2		39				1
96	0.42%		8.11%				0.21%
97			0.56				1.00
98	28		34	12	4	2	6
99	2.74%		3.32%	1.17%	0.39%	0.20%	0.59%
100	5		11	4	1	3	4
101	1.36%		3.00%	1.09%	0.27%	0.82%	1.09%
102	0.18		0.32	0.33	0.25	1.50	0.67
103			10		3	4	1
104			6.06%		1.82%	2.42%	0.61%
105			20		1	4	1
106			12.66%		0.63%	2.53%	0.63%
107			2.00		0.33	1.00	1.00
108			23	1	23	90	5
109			1.65%	0.07%	1.65%	6.45%	0.36%
110			32	2	7	25	1
111			6.07%	0.38%	1.33%	4.74%	0.19%
112			1.39	2.00	0.30	0.28	0.20
113	8		14	2	3	28	1
114	1.97%		3.44%	0.49%	0.74%	6.88%	0.25%
115	1		23	1	3	40	1
116	0.58%		13.29%	0.58%	1.73%	23.12%	0.58%
117	0.13		1.64	0.50	1.00	1.43	1.00
118			46			30	3
119			8.32%			5.42%	0.54%
120			4			38	1
121			1.44%			13.72%	0.36%
122			0.09			1.27	0.33

	U	V	W	X	Y	Z	AA
1			SHREDDERS				
2	Ceratapagonidae	Hydracarina	Doddsia	Zapada	Paracapnia	Eclisocosmoecus	Eclisomya
3							
4							
5							
6							
7							
8				27			
9				1.44%			
10				2			
11				0.44%			
12				0.07			
13	29	10		34			43
14	1.40%	0.48%		1.64%			2.08%
15	2	1		1			1
16	0.41%	0.20%		0.20%			0.20%
17	0.07	0.10		0.03			0.02
18				300	3		70
19				19.11%	0.19%		4.46%
20				18	1		15
21				2.00%	0.11%		1.67%
22				0.06	0.33		0.21
23			259	6	2		21
24			24.69%	0.57%	0.19%		2.00%
25			40	5	1		1
26			8.33%	1.04%	0.21%		0.21%
27			0.15	0.83	0.50		0.05
28		52		24			
29		1.42%		0.66%			
30		14		6			
31		3.11%		1.33%			
32		0.27		0.25			
33		15		23			156
34		0.82%		1.26%			8.52%
35		1		2			7
36		0.31%		0.63%			2.20%
37		0.07		0.09			0.04
38		12		34			73
39		1.50%		4.26%			9.15%
40		1		13			66
41		0.34%		4.36%			22.15%
42		0.08		0.38			0.90
43		9					26
44		4.41%					12.75%
45		1					143
46		0.09%					12.69%
47		0.11					5.50
48	1			10			50
49	0.11%			1.08%			5.38%
50	1			9			1
51	0.13%			1.17%			0.13%
52	1.00			0.90			0.02
53	7	46		64			37
54	0.37%	2.43%		3.38%			1.96%
55	1	1		3			1
56	0.15%	0.15%		0.44%			0.15%
57	0.14	0.02		0.05			0.03
58		2		2			
59		0.60%		0.60%			
60		1		1			
61		0.40%		0.40%			
62		0.50		0.50			
63				1	1		20
64				0.15%	0.15%		3.10%
65				1	1		1
66				0.12%	0.12%		0.12%
67				1.00	1.00		0.05

	U	V	W	X	Y	Z	AA
68				73			
69				3.77%			
70				2			
71				0.34%			
72				0.03			
73		15		58			66
74		0.59%		2.26%			2.58%
75		1		8			13
76		0.19%		1.48%			2.41%
77		0.07		0.14			0.20
78		10		131			47
79		1.36%		17.85%			6.40%
80		1		26			122
81		0.17%		4.33%			20.33%
82		0.10		0.20			2.60
83		10					
84		3.98%					
85		1					
86		0.22%					
87		0.10					
88		53					12
89		6.43%					1.46%
90		1					4
91		0.17%					0.69%
92		0.02					0.33
93	8	24		14			3
94	0.85%	2.55%		1.48%			0.32%
95	1	1		1			
96	0.21%	0.21%		0.21%			
97	0.13	0.04		0.07			
98	3	14		17			
99	0.29%	1.37%		1.66%			
100	1	2		1			
101	0.27%	0.54%		0.27%			
102	0.33	0.14		0.06			
103		2		2	1		
104		1.21%		1.21%	0.61%		
105		1		1	1		
106		0.63%		0.63%	0.63%		
107		0.50		0.50	1.00		
108		16		182		5	12
109		1.15%		13.05%		0.36%	0.86%
110		1		3		1	1
111		0.19%		0.57%		0.19%	0.19%
112		0.06		0.02		0.20	0.08
113	1			141		14	
114	0.25%			34.64%		3.44%	
115	1			15		6	
116	0.58%			8.67%		3.47%	
117	1.00			0.11		0.43	
118	4	5		131			12
119	0.72%	0.90%		23.69%			2.17%
120	1	1		26			6
121	0.36%	0.36%		9.39%			2.17%
122	0.25	0.20		0.20			0.50

	AB	AC	AD	AE	AF	AG	AH
1							
2	Onocosmoecus	Chyranda	Desmona	Grensia	Hydatophylax	Limnephilus	Tipulidae
3							3
4							1.35%
5							1
6							0.38%
7							0.33
8							8
9							0.43%
10							1
11							0.22%
12							0.13
13		2					13
14		0.10%					0.63%
15		1					10
16		0.20%					2.04%
17		0.50					0.77
18							5
19							0.32%
20							2
21							0.22%
22							0.40
23							4
24							0.38%
25							1
26							0.21%
27							0.25
28							12
29							0.33%
30							1
31							0.22%
32							0.08
33							1
34							0.05%
35							1
36							0.31%
37							1.00
38							
39							
40							
41							
42							
43		1					
44		0.49%					
45		2					
46		0.18%					
47		2.00					
48	1						1
49	0.11%						0.11%
50	6						1
51	0.78%						0.13%
52	6.00						1.00
53		1					5
54		0.05%					0.26%
55		1					1
56		0.15%					0.15%
57		1.00					0.20
58					13		1
59					3.87%		0.30%
60					68		1
61					26.98%		0.40%
62					5.23		1.00
63	12						4
64	1.86%						0.62%
65	166						1
66	20.29%						0.12%
67	13.83						0.25

	AB	AC	AD	AE	AF	AG	AH
68							12
69							0.62%
70							1
71							0.17%
72							0.08
73							3
74							0.12%
75							1
76							0.19%
77							0.33
78			1				1
79			0.14%				0.14%
80			1				45
81			0.17%				7.50%
82			1.00				45.00
83							1
84							0.10%
85							1
86							0.22%
87							1.00
88							
89							
90							
91							
92							
93							7
94							0.74%
95							1
96							0.21%
97							0.14
98							3
99							0.29%
100							12
101							3.27%
102							4.00
103	7						17
104	4.24%						10.30%
105	70						1
106	44.30%						0.63%
107	10.00						0.06
108							1
109							0.07%
110							21
111							3.98%
112							21.00
113							
114							
115							
116							
117							
118		1					1
119		0.18%					0.18%
120		1					1
121		0.36%					0.36%
122		1.00					1.00

	AI	AJ	AK	AL	AM	AN	AO	AP
1	FILTERERS					SUMMARY STATISTICS		
2	Arctopsyche	Hydropsyche	Brachycentrus	Simuliidae	Pelecypoda	#Invertebrate	Wt.-gm	Ave.. Wt/insect
3	39		16	42		223		
4	17.49%		7.17%	18.83%				
5	78			19			261	
6	29.89%			7.28%				
7	2.00			0.45				1.17
8	53		233	167		1869		
9	2.84%		12.47%	8.94%				
10	25		23	3			450	
11	5.56%		5.11%	0.67%				
12	0.47		0.10	0.02				0.24
13	191	3	69	42	94	2068		
14	9.24%	0.15%	3.34%	2.03%	4.55%			
15	122	1	21	7	24		494	
16	24.85%	0.20%	4.28%	1.43%	4.89%			
17	0.64	0.33	0.30	0.17	0.26			0.24
18	87		52	5		1570		
19	5.54%		3.31%	0.32%				
20	77		117	1			902	
21	8.56%		13.00%	0.11%				
22	0.89		2.25	0.20				0.57
23				5		1049		
24				0.48%				
25				5			437	
26				1.04%				
27				1.00				0.42
28			16	28		3653		
29			0.44%	0.77%				
30			73	1			441	
31			16.22%	0.22%				
32			4.56	0.04				0.12
33				42		1831		
34				2.29%				
35				19			317	
36				5.97%				
37				0.45				0.17
38				28		798		
39				3.51%				
40				7			281	
41				2.35%				
42				0.25				0.35
43			22	22		204		
44			10.78%	10.78%				
45			173	28			1127	
46			15.35%	2.48%				
47			7.86	1.27				5.52
48			41	144		929		
49			4.41%	15.50%				
50			8	20			749	
51			1.04%	2.60%				
52			0.20	0.14				0.81
53			139	73	22	1892		
54			7.35%	3.86%	1.16%			
55			81	17	1		684	
56			11.82%	2.48%	0.00%			
57			0.58	0.23	0.05			0.36
58			46	1		336		
59			13.69%	0.30%				
60			122	1			252	
61			48.41%	0.40%				
62			2.65	1.00				0.75
63	1		33	46		646		
64	0.15%		5.11%	7.12%				
65	1		37	19			818	
66	0.12%		4.52%	2.32%				
67	1.00		1.12	0.41				1.27

	AI	AJ	AK	AL	AM	AN	AO	AP
68	3		111	139		1935		
69	0.16%		5.74%	7.18%				
70	1		45	27			591	
71	0.17%		7.61%	4.57%				
72	0.33		0.41	0.19				0.31
73	3		120	122		2562		
74	0.12%		4.68%	4.76%				
75	1		48	12			539	
76	0.19%		8.91%	2.23%				
77	0.33		0.40	0.10				0.21
78	3		25	4		734		
79	0.41%		3.41%	0.54%				
80	12		142	1			601	
81	2.00%		23.67%	0.17%				
82	4.00		5.68	0.25				0.82
83			48	9		251		
84			19.12%	3.59%				
85			175	1			453	
86			38.63%	0.22%				
87			3.65	0.11				1.80
88			158	21		824		
89			19.17%	2.55%				
90			11	3			578	
91			1.90%	0.52%				
92			0.07	0.14				0.70
93			98	196		943		
94			10.39%	20.78%				
95			16	89			483	
96			3.33%	18.50%				
97			0.16	0.45				0.51
98			202		5	1023		
99			19.75%		0.49%			
100			147		6		367	
101			40.05%		1.63%			
102			0.73		1.20			0.36
103			4	7		165		
104			2.42%	4.24%				
105			10	4			151	
106			6.33%	2.53%				
107			2.50	0.57				0.92
108	2		494	44	2	1395		
109	0.14%		35.41%	3.15%	0.14%			
110	8		225	9	1		527	
111	1.52%		42.69%	1.71%	0.19%			
112	4.00		0.46	0.20	0.50			0.38
113	1	1				407		
114	0.25%	0.25%						
115	5	2					173	
116	2.89%	1.16%						
117	5.00	2.00						0.43
118	5		154	2		553		
119	0.90%		27.85%	0.36%				
120	46		127	1			277	
121	16.61%		45.85%	0.36%				
122	9.20		0.82	0.50				0.50

	A	B	C	D	E	F	G
1			COLLECTOR-GATHERERS				
2	Date/Stream/Year	Code	Ameletus	Baetis	Epeorus	Rithrogena	Ephemerella
3	Byers-April-1990	#	1	164		57	564
4		%#'s	0.04%	6.28%		2.18%	21.59%
5		wt mg	1	13		15	602
6		%dry wt	0.03%	0.35%		0.40%	16.13%
7		wt/invert	1.00	0.08		0.26	1.07
8	Byers-June-1990	#	1	632		9	160
9		%#'s	0.04%	25.54%		0.36%	6.46%
10		wt mg	1	61		4	273
11		%dry wt	0.05%	3.30%		0.22%	14.76%
12		wt/invert	1.00	0.10		0.44	1.71
13	Byers-August-1990	#		173			593
14		%#'s		5.40%			18.50%
15		wt mg		41			230
16		%dry wt		3.10%			17.37%
17		wt/invert		4.22			2.58
18	Byers-October-1990	#		10	4		590
19		%#'s		0.27%	0.11%		16.16%
20		wt mg		4	1		405
21		%dry wt		0.20%	0.05%		20.72%
22		wt/invert		0.40	0.25		0.69
23	E.F. Chulitna -April-1990	#	20	360			13
24		%#'s	0.85%	15.28%			0.55%
25		wt mg	3	44			36
26		%dry wt	0.19%	2.72%			2.23%
27		wt/invert	0.15	0.12			2.77
28	E.F. Chulitna-June-1990	#	6	2849			9
29		%#'s	0.16%	77.97%			0.25%
30		wt mg	4	705			14
31		%dry wt	0.40%	69.87%			1.39%
32		wt/invert	0.67	0.25			1.56
33	E.F. Chulitna-August-1990	#	1	189			14
34		%#'s	0.02%	3.83%			0.28%
35		wt mg	1	44			1
36		%dry wt	0.03%	1.52%			0.03%
37		wt/invert	1.00	0.23			0.07
38	E.F. Chulitna-October-1990	#	6	2			30
39		%#'s	0.33%	0.11%			1.66%
40		wt mg	1	1			28
41		%dry wt	0.12%	0.12%			3.29%
42		wt/invert	0.17	0.50			0.93
43	Honolulu-April-1990	#	10	1001			
44		%#'s	0.33%	33.33%			
45		wt mg	5	169			
46		%dry wt	0.22%	7.37%			
47		wt/invert	0.50	0.17			
48	Honolulu-June-1990	#	1	82			
49		%#'s	0.02%	1.51%			
50		wt mg	1	35			
51		%dry wt	0.04%	1.55%			
52		wt/invert	1.00	0.43			
53	Honolulu-August-1990	#	157	1430			
54		%#'s	3.29%	29.99%			
55		wt mg	110	261			
56		%dry wt	5.87%	13.92%			
57		wt/invert	0.70	0.18			
58	Honolulu-October-1990	#	120	14			
59		%#'s	5.11%	0.60%			
60		wt mg	46	6			
61		%dry wt	3.22%	0.42%			
62		wt/invert	0.38	0.43			
63	L. Pass-April-1990	#		355		7	578
64		%#'s		14.03%		0.28%	22.85%
65		wt mg		67		1	483
66		%dry wt		4.09%		0.06%	29.49%
67		wt/bug		0.19		0.14	0.84
68	L. Pass-June-1990	#	1	114			34
69		%#'s	0.06%	7.20%			2.15%
70		wt mg	1	26			51
71		%dry wt	0.14%	3.66%			7.18%
72		wt/bug	1.00	0.23			1.50
73	L. Pass-August-1990	#	85	28			562
74		%#'s	3.19%	1.05%			21.10%
75		wt mg	13	4			48
76		%dry wt	0.02	0.01			0.06
77		wt/bug	0.15	0.14			0.09
78	L. Pass-October-1990	#			7	6	448
79		%#'s			0.27%	0.23%	17.09%
80		wt mg			1	3	176
81		%dry wt			0.12%	0.37%	21.95%
82		wt/bug			0.14	0.50	0.39
83	L.Troublesome-April-1990	#	5	790		21	667

	A	B	C	D	E	F	G
84		%#'s	0.15%	23.46%		0.62%	19.80%
85		wt mg	1	177		6	734
86		%dry wt	0.04%	6.49%		0.22%	26.91%
87		wt./invert	0.20	0.22		0.29	1.10
88	L.Troublesome-June-1990	#	1	350		1	32
89		%#'s	0.04%	14.33%		0.04%	1.31%
90		wt mg	1	53		1	60
91		%dry wt	0.00	0.05		0.00	0.06
92		wt./invert	1.00	0.15		1.00	1.88
93	L.Troublesome-August-1990	#		333			704
94		%#'s		7.46%			15.76%
95		wt mg		68			88
96		%dry wt		5.92%			7.67%
97		wt./invert		0.20			0.13
98	L.Troublesome-October-1990	#	2	3		9	52
99		%#'s	0.26%	0.39%		1.16%	6.69%
100		wt mg	1	1		1	25
101		%dry wt	0.30%	0.30%		0.30%	7.62%
102		wt./invert	0.50	0.33		0.11	0.48
103	M.F. Chulitna -April-1990		3	53			267
104		%#'s	0.09%	1.59%			8.01%
105		wt mg	1	6			484
106		%dry wt	0.03%	0.21%			16.92%
107		wt/invert	0.33	0.11			1.81
108	M.F. Chulitna-June-1990	#	3	2881			27
109		%#'s	0.07%	66.02%			0.62%
110		wt mg	4	538			69
111		%dry wt	0.31%	41.6[illegible]%			5.34%
112		wt/invert	1.33	0.19			2.56
113	M.F. Chulitna-August-1990	#	9	1023			22
114		%#'s	0.30%	33.86%			0.73%
115		wt mg	2	154			2
116		%dry wt	0.15%	11.76%			0.15%
117		wt/bug	0.22	0.15			0.09
118	M.F. Chulitna-October-1990	#	4	3			50
119		%#'s	0.49%	0.37%			6.12%
120		wt mg	1	1			27
121		%dry wt	0.43%	0.43%			11.54%
122		wt/invert	0.25	0.33			0.54
123	U. Pass-April-1990	#	1	834		2	677
124		%#'s	0.02%	17.51%		0.04%	14.22%
125		wt mg	1	58		1	573
126		%dry wt	0.07%	4.26%		0.07%	42.13%
127		wt/invert	1.00	0.07		0.50	0.85
128	U. Pass-June-1990	#		400		1	118
129		%#'s		18.49%		0.05%	5.46%
130		wt mg		71		1	98
131		%dry wt		12.54%		0.18%	17.31%
132		wt/invert		0.18		1.00	0.83
133	U. Pass-August-1990	#	5	18			2156
134		%#'s	0.13%	0.48%			57.14%
135		wt mg	1	1			163
136		%dry wt	0.15%	0.15%			24.11%
137		wt/invert	0.20	0.06			0.08
138	U. Pass-October-1990	#		5	16	1	645
139		%#'s		0.14%	0.44%	0.03%	17.76%
140		wt mg		1	1	1	200
141		%dry wt		0.09%	0.09%	0.09%	18.54%
142		wt/invert		0.20	0.06	1.00	0.31
143	U.Troublesome-April-1990	#	9	180			289
144		%#'s	0.57%	11.44%			18.36%
145		wt mg	1	18			203
146		%dry wt	0.07%	1.27%			14.32%
147		wt/invert	0.11	0.10			0.70
148	U.Troublesome-June-1990	#	3	186			69
149		%#'s	0.17%	10.81%			4.01%
150		wt mg	4	28			94
151		%dry wt	0.67%	4.66%			15.64%
152		wt/invert	1.33	0.15			1.36
153	U.Troublesome-August-1990	#		32			200
154		%#'s		1.17%			7.34%
155		wt mg		1			12
156		%dry wt		0.10%			1.19%
157		wt/invert		0.03			0.06
158	U.Troublesome-October-1990	#	2	29			188
159		%#'s	0.06%	0.85%			5.49%
160		wt mg	1	2			74
161		%dry wt	0.09%	0.19%			7.03%
162		wt/invert	0.50	0.07			0.39

	H	I	J	K	L	M	N
1							
2	Amiocentrus	Psychoglypha	Pericoma	Chironomidae	Oligochaete	Turbellaria	Nematoda
3			1	205			1
4			0.04%	7.85%			0.04%
5			1	11			1
6			0.03%	0.29%			0.03%
7			1.00	0.05			1.00
8	2	9		604		1	4
9	0.08%	0.36%		24.40%		0.04%	0.16%
10	1	1		28		1	1
11	0.05%	0.05%		1.51%		0.05%	0.05%
12	0.50	0.11		0.05		1.00	0.25
13				619	2		6
14				19.31%	0.06%		0.19%
15				48	56		1
16				3.63%	4.23%		0.08%
17				12.90	0.04		6.00
18		2	1	163	2	2	7
19		0.05%	0.03%	4.46%	0.05%	0.05%	0.19%
20		4	1	6	1	1	1
21		0.20%	0.05%	0.31%	0.05%	0.05%	0.05%
22		2.00	1.00	0.04	0.50	0.50	0.14
23				123			
24				5.22%			
25				18			
26				1.11%			
27				0.15			
28			1	217			
29			0.03%	5.94%			
30			1	25			
31			0.10%	2.48%			
32			1.00	0.12			
33				244			
34				4.94%			
35				24			
36				0.83%			
37				0.10			
38		1		149			
39		0.06%		8.23%			
40		6		54			
41		0.70%		6.34%			
42		6.00		0.36			
43				121		12	
44				4.03%		0.40%	
45				30		7	
46				1.31%		0.31%	
47				0.25		0.58	
48				384			
49				7.06%			
50				94			
51				4.17%			
52				0.24			
53				281			
54				5.89%			
55				152			
56				8.11%			
57				0.54			
58				330			
59				14.06%			
60				210			
61				14.70%			
62				0.64			
63				239			
64				9.45%			
65				18			
66				1.10%			
67				0.08			
68		4		260			1
69		0.25%		16.41%			0.06%
70		4		13			1
71		0.56%		1.83%			0.14%
72		1.00		0.05			1.00
73		7		203			
74		0.26%		7.62%			
75		17		19			
76		0.02		0.02			
77		2.43		0.09			
78				126	1		8
79				4.81%	0.04%		0.31%
80				16	7		1
81				2.00%	0.87%		0.12%
82				0.13	7.00		0.13
83			2	133			

	H	I	J	K	L	M	N
84			0.06%	3.95%			
85			1	13			
86			0.04%	0.48%			
87			0.50	0.10			
88		2		89			
89		0.08%		3.64%			
90		8		6			
91		0.01		0.01			
92		4.00		0.07			
93		7	1	535			
94		0.16%	0.02%	11.98%			
95		39	1	141			
96		3.40%	0.09%	12.28%			
97		5.57	1.00	0.26			
98				51			
99				6.56%			
100				3			
101				0.91%			
102				0.06			
103				148			
104				4.44%			
105				53			
106				1.85%			
107				0.36			
108				201			
109				4.61%			
110				15			
111				1.16%			
112				0.07			
113		7		310			2
114		0.23%		10.26%			0.07%
115		20		28			1
116		1.53%		2.14%			0.08%
117		2.86		0.09			0.50
118				70			
119				8.57%			
120				14			
121				5.98%			
122				0.20			
123				1954			
124				41.03%			
125				136			
126				10.00%			
127				0.07			
128				160			
129				7.40%			
130				9			
131				1.59%			
132				0.06			
133		38		162			5
134		1.01%		4.29%			0.13%
135		156		11			1
136		23.08%		1.63%			0.15%
137		4.11		0.07			0.20
138		2	1	1159			83
139		0.06%	0.03%	31.92%			2.29%
140		2	1	18			1
141		0.19%	0.09%	1.67%			0.09%
142		1.00	1.00	0.02			0.01
143				172			
144				10.93%			
145				9			
146				0.63%			
147				0.05			
148			1	278			
149			0.06%	16.15%			
150			1	10			
151			0.17%	1.66%			
152			1.00	0.04			
153		19		236			4
154		0.70%		8.66%			0.15%
155		63		15			1
156		6.24%		1.49%			0.10%
157		3.32		0.06			0.25
158				470			15
159				13.72%			0.44%
160				7			1
161				0.66%			0.09%
162				0.01			0.07

	O	P	Q	R	S	T	U
1	SCRAPERS						
2	Cinyrmula	Heptagenia	Ironodes	Glossasoma	Oxyethira	Apatania	Gastropoda
3	24	124	25	49		6	
4	0.92%	4.75%	0.96%	1.88%		0.23%	
5	2	62	55	20		5	
6	0.05%	1.66%	1.47%	0.54%		0.13%	
7	0.08	0.50	2.20	0.41		0.83	
8	150	13		15	4	31	6
9	6.06%	0.53%		0.61%	0.16%	1.25%	0.24%
10	22	11		11	1	7	1
11	1.19%	0.59%		0.59%	0.05%	0.38%	0.05%
12	0.15	0.85		0.73	0.25	0.23	0.17
13	89	49	17	245	1	142	3
14	2.78%	1.53%	0.53%	7.64%	0.03%	4.43%	0.09%
15	18	19	6	141	1	54	3
16	1.35%	1.44%	0.45%	10.65%	0.08%	4.08%	0.23%
17	4.94	2.58	2.83	1.74	1.00	2.63	1.00
18	27	122	27	81	7	116	6
19	0.74%	3.34%	0.74%	2.22%		3.18%	0.16%
20	1	106	30	23	1	78	18
21	0.05%	5.42%	1.53%	1.18%	0.05%	3.99%	0.92%
22	0.04	0.87	1.11	0.28	0.14	0.67	3.00
23	20		202				
24	0.85%		8.57%				
25	1		328				
26	0.06%		20.30%				
27	0.05		1.62				
28	266		5	1			
29	7.28%		0.14%	0.03%			
30	13		59	1			
31	1.29%		5.85%	0.10%			
32	0.05		11.80	1.00			
33	260		1990	19			
34	5.26%		40.29%	0.38%			
35	153		581	1			
36	5.28%		20.06%	0.03%			
37	0.59		0.29	0.05			
38			319	4			1
39			17.62%	0.22%			0.06%
40			265	1			1
41			31.10%	0.12%			0.12%
42			0.83	0.25			1.00
43	3		148	62			
44	0.10%		4.93%	2.06%			
45	3		438	40			
46	0.13%		19.10%	1.74%			
47	1.00		2.96	0.65			
48	364		3699	69			3
49	6.69%		67.97%	1.27%			0.06%
50	335		1107	4			3
51	14.86%		49.09%	0.18%			0.13%
52	0.92		0.30	0.06			1.00
53	2143		4	3			1
54	44.95%		0.08%	0.06%			0.02%
55	177		9	1			1
56	9.44%		0.48%	0.05%			0.05%
57	0.08		2.25	0.33			1.00
58	1		497	13			3
59	0.04%		21.18%	0.55%			0.13%
60	1		324	4			1
61	0.07%		22.67%	0.28%			0.07%
62	1.00		0.65	0.31			0.33
63	69	9	1	16			
64	2.73%	0.36%	0.04%	0.63%			
65	2	23	1	5			
66	0.12%	1.40%	0.06%	0.31%			
67	0.03	2.56	1.00	0.31			
68	523	2	2	3			2
69	33.02%	0.13%	0.13%	0.19%			0.13%
70	57	1	13	1			1
71	8.03%	0.14%	1.83%	0.14%			0.14%
72	0.11	0.50	6.50	0.33			0.50
73	136	19	106	145	1	7	2
74	5.11%	0.71%	3.98%	5.44%	0.04%	0.26%	0.08%
75	18	3	48	26	1	7	4
76	0.02	0.00	0.06	0.03	0.00	0.01	0.01
77	0.13	0.16	0.45	0.18	1.00	1.00	2.00
78	17	36		30		6	6
79	0.65%	1.37%		1.14%		0.23%	0.23%
80	1	6		6		3	13
81	0.12%	0.75%		0.75%		0.37%	1.62%
82	0.06	0.17		0.20		0.50	2.17
83	170	1	85	36			

	O	P	Q	R	S	T	U
84	5.05%	0.03%	2.52%	1.07%			
85	10	1	238	25			
86	0.37%	0.04%	8.72%	0.92%			
87	0.06	1.00	2.80	0.69			
88	1381		44	4		1	
89	56.53%		1.80%	0.16%		0.04%	
90	107		185	1		1	
91	0.10		0.17	0.00		0.00	
92	0.08		4.20	0.25		1.00	
93	24	3	622	174		3	2
94	0.54%	0.07%	13.93%	3.90%		0.07%	0.04%
95	16	1	143	63		1	1
96	1.39%	0.09%	12.46%	5.49%		0.09%	0.09%
97	0.67	0.33	0.23	0.36		0.33	0.50
98	2		57	7		1	
99	0.26%		7.34%	0.90%		0.13%	
100	1		17	6		1	
101	0.30%		5.18%	1.83%		0.30%	
102	0.50		0.30	0.86		1.00	
103	57	10	186	41			6
104	1.71%	0.30%	5.58%	1.23%			
105	1	5	245	36			5
106	0.03%	0.17%	8.56%	1.26%			
107	0.02	0.50	1.32	0.88			
108	938		4	2			1
109	21.49%		0.09%	0.05%			0.02%
110	68		18	1			1
111	5.27%		1.39%	0.08%			0.08%
112	0.07		4.50	0.50			1.00
113	128		589	26			1
114	4.24%		19.50%	0.86%			0.03%
115	92		180	1			1
116	7.02%		13.74%	0.08%			0.08%
117	0.72		0.31	0.04			1.00
118	3		62	21			1
119	0.37%		7.59%	2.57%			0.12%
120	3		48	3			1
121	1.28%		20.51%	1.28%			0.43%
122	1.00		0.77	0.14			1.00
123	52	63		127		3	
124	1.09%	1.32%		2.67%		0.06%	
125	1	16		50		5	
126	0.07%	1.18%		3.68%		0.37%	
127	0.02	0.25		0.39		1.67	
128	371	38		6	1	1	1
129	17.15%	1.76%		0.28%	0.05%	0.05%	0.05%
130	28	21		5	1	1	1
131	4.95%	3.71%		0.88%	0.18%	0.18%	0.18%
132	0.08	0.55		0.83	1.00	1.00	1.00
133	26	159	20	215	3	120	
134	0.69%	4.21%	0.53%	5.70%	0.08%	3.18%	
135	7	7	3	12	1	22	
136	1.04%	1.04%	0.44%	1.78%	0.15%	3.25%	
137	0.27	0.04	0.15	0.06	0.33	0.18	
138	13	242		310		78	1
139	0.36%	6.66%		8.54%		2.15%	0.03%
140	1	26		40		39	1
141	0.09%	2.41%		3.71%		3.61%	0.09%
142	0.08	0.11		0.13		0.50	1.00
143	49	9	116	6			
144	3.11%	0.57%	7.37%	0.38%			
145	1	2	116	2			
146	0.07%	0.14%	8.18%	0.14%			
147	0.02	0.22	1.00	0.33			
148	505	3	32	1			
149	29.34%	0.17%	1.86%	0.06%			
150	38	2	57	1			
151	6.32%	0.33%	9.48%	0.17%			
152	0.08	0.67	1.78	1.00			
153	32		175	209		5	1
154	1.17%		6.42%	7.67%		0.18%	0.04%
155	6		20	11		1	1
156	0.59%		1.96%	1.09%		0.10%	0.10%
157	0.19		0.11	0.05		0.20	1.00
158	16	9	295	46		2	3
159	0.47%	0.26%	8.61%	1.34%		0.06%	0.09%
160	1	1	117	13		1	3
161	0.09%	0.09%	11.11%	1.23%		0.09%	0.28%
162	0.06	0.11	0.40	0.28		0.50	1.00

	V	W	X	Y	Z	AA	AB
1	PREDATORS						
2	Drunella	Arcynopteryx	Isoperla	Neaviperla	Plumiperla	Rhyacophila	Dicranota
3	100		47		11	1	12
4	3.83%		1.80%		0.42%	0.04%	0.46%
5	81		9		6	7	11
6	2.17%		0.24%		0.16%	0.19%	0.29%
7	0.81		0.19		0.55	7.00	0.92
8	140		27		143		33
9	5.66%		1.09%		5.78%		1.33%
10	424		15		76		8
11	22.92%		0.81%		4.11%		0.43%
12	3.03		0.56		0.53		0.24
13	100	23	6		14	1	5
14	3.12%	0.72%	0.19%		0.44%	0.03%	0.16%
15	10	28	2		2	1	6
16	0.76%	2.11%	0.15%		0.15%	0.08%	0.45%
17	10.00	0.82	3.00		7.00	1.00	0.83
18	176		29		28		10
19	4.82%		0.79%		0.77%		0.27%
20	71		128		9		14
21	3.63%		6.55%		0.46%		0.72%
22	0.40		4.41		0.32		1.40
23	685		75		17	1	
24	29.07%		3.18%		0.7?%	0.04%	
25	690		42		9	1	
26	42.70%		2.60%		0.56%	0.06%	
27	1.01		0.56		0.53	1.00	
28	36		38		112		35
29	0.99%		1.04%		3.07%		0.96%
30	36		25		81		10
31	3.57%		2.48%		8.03%		0.99%
32	1.00		0.66		0.72		0.29
33	1625		2		348	1	
34	32.90%		0.04%		7.05%	0.02%	
35	1804		4		178	1	
36	62.27%		0.14%		6.14%	0.03%	
37	1.11		2.00		0.51	1.00	
38	792	3	40		6		
39	43.76%	0.17%	2.21%		0.33%		
40	192	9	24		2		
41	22.54%	1.06%	2.82%		0.23%		
42	0.24	3.00	0.60		0.33		
43	141		34		67	2	
44	4.70%		1.13%		2.23%	0.07%	
45	260		35		139	1	
46	11.34%		1.53%		6.06%	0.04%	
47	1.84		1.03		2.07	0.50	
48	215				398	5	
49	3.95%				7.31%	0.09%	
50	349				269	4	
51	15.48%				11.93%	0.18%	
52	1.62				0.68	0.80	
53	118		4		531	5	20
54	2.47%		0.08%		11.14%	0.10%	0.42%
55	321		3		763	20	3
56	17.12%		0.16%		40.69%	1.07%	0.16%
57	2.72		0.75		1.44	4.00	0.15
58	402		7		68	2	1
59	17.13%		0.30%		2.90%	0.09%	0.04%
60	166		1		41	1	1
61	11.62%		0.07%		2.87%	0.07%	0.07%
62	0.41		0.14		0.60	0.50	1.00
63	828		89		11	31	17
64	32.73%		3.52%		0.43%	1.23%	0.67%
65	678		23		1	86	6
66	41.39%		1.40%		0.06%	5.25%	0.37%
67	0.82		0.26		0.09	2.77	0.35
68	180		31		186	10	39
69	11.36%		1.96%		11.74%	0.63%	2.46%
70	309		10		106	2	11
71	43.52%		1.41%		14.93%	0.28%	1.55%
72	1.72		0.32		0.57	0.20	0.28
73	927		4	1	175	24	
74	34.81%		0.15%	0.04%	6.57%	0.90%	
75	366		1	1	45	13	
76	0.48		0.00	0.00	0.06	0.02	
77	0.39		0.25	1.00	0.26	0.54	
78	1243		34		43	19	17
79	47.42%		1.30%		1.64%	0.72%	0.65%
80	352		11		4	15	2
81	43.89%		1.37%		0.50%	1.87%	0.25%
82	0.28		0.32		0.09	0.79	0.12
83	519		34		15	46	73

	V	W	X	Y	Z	AA	AB
84	15.41%		1.01%		0.45%	1.37%	2.17%
85	582		17		4	133	62
86	21.33%		0.62%		0.15%	4.88%	2.27%
87	1.12		0.50		0.27	2.89	0.85
88	231		2		197	11	23
89	9.46%		0.08%		8.06%	0.45%	0.94%
90	452		1		172	6	4
91	0.42		0.00		0.16	0.01	0.00
92	1.96		0.50		0.87	0.55	0.17
93	1409				242	55	
94	31.55%				5.42%	1.23%	
95	363				90	35	
96	31.62%				7.84%	3.05%	
97	0.26				0.37	0.64	
98	343				6	13	9
99	44.14%				0.77%	1.67%	1.16%
100	107				2	21	2
101	32.62%				0.61%	6.40%	0.61%
102	0.31				0.33	1.62	0.22
103	1395		165		119	8	34
104	41.87%		4.95%		3.57%	0.24%	1.02%
105	896		61		79	14	30
106	31.32%		2.13%		2.76%	0.49%	1.05%
107	0.64		0.37		0.66	1.75	0.88
108	115		15		67	1	5
109	2.64%		0.34%		1.54%	0.02%	0.11%
110	287		13		27	1	2
111	22.23%		1.01%		2.09%	0.08%	0.15%
112	2.50		0.87		0.40	1.00	0.40
113	183		2		368	6	
114	6.06%		0.07%		12.18%	0.20%	
115	558		2		115	3	
116	42.60%		0.15%		8.78%	0.23%	
117	3.05		1.00		0.31	0.50	
118	232		23		13		6
119	28.40%		2.82%		1.59%		0.73%
120	49		4		2		1
121	20.94%		1.71%		0.85%		0.43%
122	0.21		0.17		0.15		0.17
123	101		140		2	6	8
124	2.12%		2.94%		0.04%	0.13%	0.17%
125	75		65		1	8	1
126	5.51%		4.78%		0.07%	0.59%	0.07%
127	0.74		0.46		0.50	1.33	0.13
128	5		28		19	3	8
129	0.23%		1.29%		0.88%	0.14%	0.37%
130	5		17		13	1	3
131	0.88%		3.00%		2.30%	0.18%	0.53%
132	1.00		0.61		0.68	0.33	0.38
133	214		4		29	3	20
134	5.67%		0.11%		0.77%	0.08%	0.53%
135	8		2		6	1	3
136	1.18%		0.30%		0.89%	0.15%	0.44%
137	0.04		0.50		0.21	0.33	0.15
138	119		27		16		42
139	3.28%		0.74%		0.44%		1.16%
140	30		8		1		7
141	2.78%		0.74%		0.09%		0.65%
142	0.25		0.30		0.06		0.17
143	37		8		2	87	5
144	2.35%		0.51%		0.13%	5.53%	0.32%
145	21		5		1	84	3
146	1.48%		0.35%		0.07%	5.92%	0.21%
147	0.57		0.63		0.50	0.97	0.60
148	16		3	2	8	60	5
149	0.93%		0.17%	0.12%	0.46%	3.49%	0.29%
150	18		2	3	3	26	5
151	3.00%		0.33%	0.50%	0.50%	4.33%	0.83%
152	1.13		0.67	1.50	0.38	0.43	1.00
153	239		10	4	5	190	1
154	8.77%		0.37%	0.15%	0.18%	6.98%	0.04%
155	24		1	2	2	65	1
156	2.38%		0.10%	0.20%	0.20%	6.44%	0.10%
157	0.10		0.10	0.50	0.40	0.34	1.00
158	187		8		14	104	11
159	5.46%		0.23%		0.41%	3.04%	0.32%
160	24		7		1	91	1
161	2.28%		0.66%		0.09%	8.64%	0.09%
162	0.13		0.88		0.07	0.88	0.09

	AC	AD	AE	AF	AG	AH	AI
1					PREDATOR		
2	Ceratopogonidae	Clinocera	Chelifera	Hydracarina	Doddsia	Malenka	Nemoura
3	3	40		17			
4	0.11%	1.53%		0.65%			
5	1	6		1			
6	0.03%	0.16%		0.03%			
7	0.33	0.15		0.06			
8	32	2	53	90			
9	1.29%	0.08%	2.14%	3.64%			
10	1	1	8	6			
11	0.05%	0.05%	0.43%	0.32%			
12	0.03	0.50	0.15	0.07			
13	9	6	76	22			
14	0.28%	0.19%	2.37%	0.69%			
15	1	1	6	1			
16	0.08%	0.08%	0.45%	0.08%			
17	9.00	6.00	12.67	22.00			
18		1	37	17	1		
19		0.03%	1.01%	0.47%	0.03%		
20		8	8	2	1		
21		0.41%	0.41%	0.10%	0.05%		
22		8.00	0.22	0.12	1.00		
23		2		2	708		
24		0.08%		0.08%	30.05%		
25		1		1	367		
26		0.06%		0.06%	22.71%		
27		0.50		0.50	0.52		
28	6		8	35			
29	0.16%		0.22%	0.96%			
30	1		3	1			
31	0.10%		0.30%	0.10%			
32	0.17		0.38	0.03			
33		2	11	82	6		
34		0.04%	0.22%	1.66%	0.12%		
35		1	1	8	1		
36		0.03%	0.03%	0.28%	0.03%		
37		0.50	0.09	0.10	0.17		
38		2	1	33	318		
39		0.11%	0.06%	1.82%	17.57%		
40		1	1	5	50		
41		0.12%	0.12%	0.59%	5.87%		
42		0.50	1.00	0.15	0.16		
43		3		7	1168		
44		0.10%		0.23%	38.89%		
45		1		1	813		
46		0.04%		0.04%	35.46%		
47		0.33		0.14	0.70		
48		1	3	17	66		
49		0.02%	0.06%	0.31%	1.21%		
50		1	1	2	2		
51		0.04%	0.04%	0.09%	0.09%		
52		1.00	0.33	0.12	0.03		
53		1	3	15			
54		0.02%	0.06%	0.31%			
55		1	1	1			
56		0.05%	0.05%	0.05%			
57		1.00	0.33	0.07			
58			1	13	605		1
59			0.04%	0.55%	25.78%		0.04%
60			1	1	108		1
61			0.07%	0.07%	7.56%		0.07%
62			1.00	0.08	0.18		1.00
63	1	3	18	5	21		
64	0.04%	0.12%	0.71%	0.20%	0.83%		
65	1	3	1	1	19		
66	0.06%	0.18%	0.06%	0.06%	1.16%		
67	1.00	1.00	0.06	0.20	0.90		
68	2	42		43			
69	0.13%	2.65%		2.71%			
70	1	15		2			
71	0.14%	2.11%		0.28%			
72	0.50	0.36		0.05			
73	8		7	29	1		
74	0.30%		0.26%	1.09%	0.04%		
75	2		1	2	1		
76	0.00		0.00	0.00	0.00		
77	0.25		0.14	0.07	1.00		
78		2	7	17	9		
79		0.08%	0.27%	0.65%	0.34%		
80		0.5	0.5	1	1		
81		0.06%	0.06%	0.12%	0.12%		
82		0.25	0.07	0.06	0.11		
83		5	8	14	110		

	AC	AD	AE	AF	AG	AH	AI
84		0.15%	0.24%	0.42%	3.27%		
85		8	1	3	140		
86		0.29%	0.04%	0.11%	5.13%		
87		1.60	0.13	0.21	1.27		
88	5		5	11	2		
89	0.20%		0.20%	0.45%	0.08%		
90	1		1	1	1		
91	0.00		0.00	0.00	0.00		
92	0.20		0.20	0.09	0.50		
93	4	1	3	47			
94	0.09%	0.02%	0.07%	1.05%			
95	1	1	1	7			
96	0.09%	0.09%	0.09%	0.61%			
97	0.25	1.00	0.33	0.15			
98			2	6	2		1
99			0.26%	0.77%	0.26%		0.13%
100			1	1	1		1
101			0.30%	0.30%	0.30%		0.30%
102			0.50	0.17	0.50		1.00
103		5		16	358		
104		0.15%		0.48%	10.74%		
105		1		1	155		
106		0.03%		0.03%	5.42%		
107		0.20		0.06	0.43		
108			52				
109			1.19%				
110			20				
111			1.55%				
112			0.38				
113	1		22	84			4
114	0.03%		0.73%	2.78%			0.13%
115	1		6	6			1
116	0.08%		0.46%	0.46%			0.08%
117	1.00		0.27	0.07			0.25
118			1	15	220		
119			0.12%	1.84%	26.93%		
120			1	1	36		
121			0.43%	0.43%	15.38%		
122			1.00	0.07	0.16		
123	10	158		204	15		
124	0.21%	3.32%		4.28%	0.31%		
125	1	10		13	20		
126	0.07%	0.74%		0.96%	1.47%		
127	0.10	0.06		0.06	1.33		
128	14		38	30			
129	0.65%		1.76%	1.39%			
130	1		6	3			
131	0.18%		1.06%	0.53%			
132	0.07		0.16	0.10			
133	162		24	122			
134	4.29%		0.64%	3.23%			
135	20		4	12			
136	2.96%		0.59%	1.78%			
137	0.12		0.17	0.10			
138	7	4	41	128	12		
139	0.19%	0.11%	1.13%	3.53%	0.33%		
140	1	1	4	12	1		
141	0.09%	0.09%	0.37%	1.11%	0.09%		
142	0.14	0.25	0.10	0.09	0.08		
143	3	2	4	37		1	
144	0.19%	0.13%	0.25%	2.35%		0.06%	
145	1	1	1	2		1	
146	0.07%	0.07%	0.07%	0.14%		0.07%	
147	0.33	0.50	0.25	0.05		1.00	
148	6	2	9	21			
149	0.35%	0.12%	0.52%	1.22%			
150	1	1	1	1			
151	0.17%	0.17%	0.17%	0.17%			
152	0.17	0.50	0.11	0.05			
153	11	3	3	43			
154	0.40%	0.11%	0.11%	1.58%			
155	1	1	1	1			
156	0.10%	0.10%	0.10%	0.10%			
157	0.09	0.33	0.33	0.02			
158	2	1	7	35			
159	0.06%	0.03%	0.20%	1.02%			
160	1	1	1	4			
161	0.09%	0.09%	0.09%	0.38%			
162	0.50	1.00	0.14	0.11			

	AJ	AK	AL	AM	AN	AO	AP
1							
2	Soyedina	Zapada	Allocapnia	Paracapnia	Amphicosmoecus	Eclisocosm.	Eclisomya
3		573	8				1
4		21.94%	0.31%				0.04%
5		254	1				5
6		6.81%	0.03%				0.13%
7		0.44	0.13				5.00
8		9					24
9		0.36%					0.97%
10		1					188
11		0.05%					10.16%
12		0.11					7.83
13		606	2				21
14		18.90%	0.06%				0.66%
15		68	1				4
16		5.13%	0.08%				0.30%
17		8.91	2.00				5.25
18		1905	1				6
19		52.16%	0.03%				0.16%
20		320	1				3
21		16.37%	0.05%				0.15%
22		0.17	1.00				0.50
23		89	32				3
24		3.78%	1.36%				0.13%
25		65	3				5
26		4.02%	0.19%				0.31%
27		0.73	0.09				1.67
28		12					
29		0.33%					
30		1					
31		0.10%					
32		0.08					
33		39	1				5
34		0.79%	0.02%				0.10%
35		3	1				1
36		0.10%	0.03%				0.03%
37		0.08	1.00				0.20
38		49	4				45
39		2.71%	0.22%				2.49%
40		23	1				183
41		2.70%	0.12%				21.48%
42		0.47	0.25				4.07
43		151	28				43
44		5.03%	0.93%				1.43%
45		155	4				189
46		6.76%	0.17%				8.24%
47		1.03	0.14				4.40
48		84					23
49		1.54%					0.42%
50		10					7
51		0.44%					0.31%
52		0.12					0.30
53		46					
54		0.96%					
55		18					
56		0.96%					
57		0.39					
58	1	145	6				108
59	0.04%	6.18%	0.26%				4.60%
60	1	78	1				430
61	0.07%	5.46%	0.07%				30.09%
62	1.00	0.54	0.17				3.98
63		27	110				10
64		1.07%	4.35%				0.40%
65		14	20				125
66		0.85%	1.22%				7.63%
67		0.52	0.18				12.50
68		13	2				2
69		0.82%	0.13%				0.13%
70		1	1				7
71		0.14%	0.14%				0.99%
72		0.08	0.50				3.50
73		45					9
74		1.69%					0.34%
75		1					2
76		0.00					0.00
77		0.02					0.22
78		322	1				7
79		12.29%	0.04%				0.27%
80		29	1				1
81		3.62%	0.12%				0.12%
82		0.09	1.00				0.14
83		521	50				18

	AJ	AK	AL	AM	AN	AO	AP
84		15.47%	1.48%				0.53%
85		339	12				18
86		12.43%	0.44%				0.66%
87		0.65	0.24				1.00
88		11	3				
89		0.45%	0.12%				
90		1	1				
91		0.00	0.00				
92		0.09	0.33				
93		218	1				11
94		4.88%	0.02%				0.25%
95		13	1				6
96		1.13%	0.09%				0.52%
97		0.06	1.00				0.55
98		139	5				1
99		17.89%	0.64%				0.13%
100		33	1				1
101		10.06%	0.30%				0.30%
102		0.24	0.20				1.00
103		359	15				38
104		10.77%	0.45%				1.14%
105		400	1				217
106		13.98%	0.03%				7.58%
107		1.11	0.07				5.71
108		10					1
109		0.23%					0.02%
110		1					1
111		0.08%					0.08%
112		0.10					1.00
113		72					1
114		2.38%					0.03%
115		7					1
116		0.53%					0.08%
117		0.10					1.00
118		27	29	2			
119		3.30%	3.55%	0.24%			
120		6	4	1			
121		2.56%	1.71%	0.43%			
122		0.22	0.14	0.50			
123		67	61				3
124		1.41%	1.28%				0.06%
125		19	16				13
126		1.40%	1.18%				0.96%
127		0.28	0.26				4.33
128		2	1				
129		0.09%	0.05%				
130		1	1				
131		0.18%	0.18%				
132		0.50	1.00				
133		20			1		3
134		0.53%			0.03%		0.08%
135		1			3		1
136		0.15%			0.44%		0.15%
137		0.05			3.00		0.33
138		85					1
139		2.34%					0.03%
140		2					1
141		0.19%					0.09%
142		0.02					1.00
143		279	25			2	12
144		17.73%	1.59%			0.13%	0.76%
145		138	4			5	72
146		9.73%	0.28%			0.35%	5.08%
147		0.49	0.16			2.50	6.00
148		156					6
149		9.06%					0.35%
150		4					11
151		0.67%					1.83%
152		0.03					1.83
153		522					29
154		19.16%					1.06%
155		31					11
156		3.07%					1.09%
157		0.06					0.38
158		1415	2			7	5
159		41.31%	0.06%			0.20%	0.15%
160		194	1			15	10
161		18.42%	0.09%			1.42%	0.95%
162		0.14	0.50			2.14	2.00

	AQ	AR	AS	AT	AU	AV	AW
1							
2	Onocosmoecus	Chyranda	Desmona	Grensia	Hydatophylax	Limnephilus	Tipula
3	32	1			1		
4	1.23%	0.04%			0.04%		
5	177	1			6		
6	4.74%	0.03%			0.16%		
7	5.53	1.00			6.00		
8	26						
9	1.05%						
10	328						
11	17.73%						
12	12.62						
13	14						8
14	0.44%						0.25%
15	1						34
16	0.08%						2.57%
17	14.00						0.24
18	32						
19	0.88%						
20	21						
21	1.07%						
22	0.66						
23				2			1
24				0.08%			0.04%
25				3			1
26				0.19%			0.06%
27				1.50			1.00
28							9
29							0.25%
30							22
31							2.18%
32							2.44
33							
34							
35							
36							
37							
38	2						
39	0.11%						
40	1						
41	0.12%						
42	0.50						
43							
44							
45							
46							
47							
48							
49							
50							
51							
52							
53							3
54							0.06%
55							32
56							1.71%
57							10.67
58							
59							
60							
61							
62							
63	54					1	
64	2.13%					0.04%	
65	6					1	
66	0.37%					0.06%	
67	0.11					1.00	
68							3
69							0.19%
70							10
71							1.41%
72							3.33
73	2						
74	0.08%						
75	2						
76	0.00						
77	1.00						
78	2						1
79	0.08%						0.04%
80	1						9
81	0.12%						1.12%
82	0.50						9.00
83	18	3					1

	AQ	AR	AS	AT	AU	AV	AW
84	0.53%	0.09%					0.03%
85	121	9					19
86	4.44%	0.33%					0.70%
87	6.72	3.00					19.00
88							
89							
90							
91							
92							
93							3
94							0.07%
95							1
96							0.09%
97							0.33
98	11			1			
99	1.42%			0.13%			
100	3			1			
101	0.91%			0.30%			
102	0.27			1.00			
103	50	6			1		
104	1.50%	0.18%			0.03%		
105	174	3			3		
106	6.08%	0.10%			0.10%		
107	3.48	0.50			3.00		
108	1						38
109	0.02%						0.87%
110	9						215
111	0.70%						16.65%
112	9.00						5.66
113							4
114							0.13%
115							73
116							5.57%
117							18.25
118	11				5		3
119	1.35%				0.61%		0.37%
120	3				5		15
121	1.28%				2.14%		6.41%
122	0.27				1.00		5.00
123	4						4
124	0.08%						0.08%
125	8						71
126	0.59%						5.22%
127	2.00						17.75
128	2						
129	0.09%						
130	2						
131	0.35%						
132	1.00						
133	1						2
134	0.03%						0.05%
135	1						3
136	0.15%						0.44%
137	1.00						1.50
138	3						
139	0.08%						
140	1						
141	0.09%						
142	0.33						
143	15	4	2				2
144	0.95%	0.25%	0.13%				0.13%
145	67	11	4				35
146	4.72%	0.78%	0.28%				2.47%
147	4.47	2.75	2.00				17.50
148							1
149							0.06%
150							3
151							0.50%
152							3.00
153	1						
154	0.04%						
155	1						
156	0.10%						
157	1.00						
158	21	2		1			1
159	0.61%	0.06%		0.03%			0.03%
160	3	1		3			1
161	0.28%	0.09%		0.28%			0.09%
162	0.14	0.50		3.00			1.00

	AX	AY	AZ	BA	BB	BC	BD	BE	BF
1	FILTERERS						SUMMARY STATISTICS		
2	Arctopsyche	Hydropsyche	Brachycentrus	Prosimulium	Simulium	Pelecypoda	#Invert	WT-gm	Ave.wt/indiv.
3	262	10	111	11		150	2612		
4	10.03%	0.38%	4.25%	0.42%		5.74%			
5	1854	15	405	4		100		3732	1.43
6	49.68%	0.40%	10.85%	0.11%		2.68%			
7	7.08	1.50	3.65	0.36		0.67			
8	10	1	159	22	2	61	2475		
9	0.40%	0.04%	6.42%	0.89%	0.08%	2.46%			
10	34	1	296	8	1	30		1850	0.75
11	1.84%	0.05%	16.00%	0.43%	0.05%	1.62%			
12	3.40	1.00	1.86	0.36	0.50	0.49			
13	108	11	178	1		56	3206		
14	3.37%	0.34%	5.55%	0.03%		1.75%			
15	279	17	194	1		49		1324	0.41
16	21.07%	1.28%	14.65%	0.08%		3.70%			
17	0.39	0.65	0.92	1.00		1.14			
18	44	8	112			82	3656		
19	1.20%	0.22%	3.07%			2.25%			
20	313	10	323			42		1955	0.53
21	16.01%	0.51%	16.52%			2.15%			
22	7.11	1.25	2.88			0.51			
23				1			2356		
24				0.04%					
25				1				1619	0.69
26				0.06%					
27				1.00					
28				9			3654		
29				0.25%					
30				7				1009	0.28
31				0.69%					
32				0.78					
33				100			4939		
34				2.02%					
35				89				2897	0.59
36				3.07%					
37				0.89					
38				3			1810		
39				0.17%					
40				3				852	0.47
41				0.35%					
42				1.00					
43				2			3003		
44				0.07%					
45				1				2291	0.76
46				0.04%					
47				0.50					
48				28			5442		
49				0.51%					
50				31				2255	0.41
51				1.37%					
52				1.11					
53				3			4768		
54				0.06%					
55				1				1875	0.39
56				0.05%					
57				0.33					
58				9			2347		
59				0.38%					
60				6				1429	0.61
61				0.42%					
62				0.67					
63			17	12		1	2530		
64			0.67%	0.47%		0.04%			
65			51	1		1		1638	0.65
66			3.11%	0.06%		0.06%			
67			3.00	0.08		1.00			
68			56	25	1	3	1584		
69			3.54%	1.58%	0.06%	0.19%			
70			54	10	1	1		710	0.45
71			7.61%	1.41%	0.14%	0.14%			
72			0.96	0.40	1.00	0.33			
73			74	54		2	2663		
74			2.78%	2.03%		0.08%			
75			101	21		2		769	0.29
76			0.13	0.03		0.00			
77			1.36	0.39		1.00			
78		2	200	2		2	2621		
79		0.08%	7.63%	0.08%		0.08%			
80		2	137	1		1		802	0.31
81		0.25%	17.08%	0.12%		0.12%			
82		1.00	0.59	0.50		0.50			
83	6		12	5			3368		

	AX	AY	AZ	BA	BB	BC	BD	BE	BF
84	0.15%		0.36%	0.15%					
85	36		17	1				2728	0.81
86	1.32%		0.62%	0.04%					
87	6.00		1.42	0.20					
88	4		32	4			2446		
89	0.16%		1.31%	0.16%					
90	4		16	1				1065	0.44
91	0.00		0.01	0.00					
92	1.00		0.50	0.25					
93	19		26	9	10		4466		
94	0.43%		0.58%	0.20%	0.22%				
95	14		48	3	2			1148	0.26
96	1.22%		4.18%	0.26%	0.17%				
97	0.74		1.85	0.33	0.20				
98	8		45	1			777		
99	1.03%		5.79%	0.13%					
100	34		62	1				328	0.42
101	10.37%		18.90%	0.30%					
102	4.25		1.38	1.00					
103			2				3342		
104			0.06%						
105			1					2872	0.86
106			0.03%						
107			0.50						
108				3			4365		
109				0.07%					
110				1				1291	0.30
111				0.08%					
112				0.33					
113			10	147			3021		
114			0.33%	4.87%					
115			8	50				1312	0.43
116			0.61%	3.82%					
117			0.80	0.34					
118			2	11	2	1	817		
119			0.24%	1.35%	0.24%	0.12%			
120			2	4	1	1		234	0.29
121			0.85%	1.71%	0.43%	0.43%			
122			1.00	0.36	0.50	1.00			
123			151	110		5	4762		
124			3.17%	2.31%		0.10%			
125			182	12		2		1358	0.29
126			13.38%	0.88%		0.15%			
127			1.21	0.11		0.40			
128			94	818		4	2163		
129			4.35%	37.82%		0.18%			
130			175	99		1		564	0.26
131			30.92%	17.49%		0.18%			
132			1.86	0.12		0.25			
133			203	11		27	3773		
134			5.38%	0.29%		0.72%			
135			203	7		14		674	0.18
136			30.03%	1.04%		2.07%			
137			1.00	0.64		0.52			
138		1	521			68	3631		
139		0.03%	14.35%			1.87%			
140		1	638			39		1079	0.30
141		0.09%	59.13%			3.61%			
142		1.00	1.22			0.57			
143	34		151	41			1583		
144	2.16%		9.59%	2.60%					
145	202		407	4				1421	0.90
146	14.25%		28.70%	0.28%					
147	5.94		2.70	0.10					
148	15		275	58			1721		
149	0.87%		15.98%	3.37%					
150	44		214	29				601	0.35
151	7.32%		35.61%	4.83%					
152	2.93		0.78	0.50					
153	126		610	12		2	2724		
154	4.63%		22.39%	0.44%		0.07%			
155	331		404	1		1		1010	0.37
156	32.77%		40.00%	0.10%		0.10%			
157	2.63		0.66	0.08		0.50			
158	56	1	450	18		3	3426		
159	1.64%	0.03%	13.14%	0.53%		0.09%			
160	189	3	276	2		2		1052	0.31
161	17.95%	0.28%	26.21%	0.19%		0.19%			
162	3.38	3.00	0.61	0.11		0.67			

APPENDIX B-Stable Isotope Data

Stream/Date/Year	Funct. Group	Genera	% Community WT.	∂N	∂C
L.Pass-April-1988	Coll./Gath.	Baetis	0.17%	3.04	-32.26
	Coll./Gath.	Ephemerella	51.38%	3.86	-29.80
	Scraper	Heptageniidae	2.22%	3.29	-29.60
	Predator	Drunella	11.09%	4.55	-30.75
	Predator	Isoperla	2.22%	5.38	-33.40
	Shredder	Ecclisomyia	12.69%	3.47	-29.74
	Filterer	Prosimulium	2.48%	3.44	-30.64
	Filterer	Brachycentrus	15.35%	4.23	-32.62
		% total biomass	97.60%		
		Calculated isotope ratios for whole stream		3.96	-30.45
L.Pass-June-1988	Coll./Gath.	Ephemerella	1.82%	2.34	-30.05
	Coll./Gath.	Chironomidae	7.02%	3.70	-26.87
	Scraper	Heptageniidae	3.64%	3.38	-28.67
	Predator	Drunella	68.05%	2.99	-29.36
	Predator	Plumiperla	8.31%	3.13	-28.25
	Filterer	Prosimulium	2.60%	5.15	-27.91
	Filterer	Brachycentrus	1.04%	4.27	-30.57
		% total biomass	92.48%		
		Calculated isotope ratios for whole stream		3.13	-29.03
L.Pass-August-1988	Coll./Gath.	Chironomidae	14.60%	4.90	-26.61
	Coll./Gath.	Psychoglypha	40.29%	3.09	-30.26
	Scraper	Heptageniidae	2.34%	4.62	-29.58
	Scraper	Glossosoma	4.82%	3.74	-29.26
	Predator	Drunella	15.33%	4.66	-27.95
	Predator	Isoperla	0.44%	6.36	-26.98
	Shredder	Ecclisomyia	0.15%	3.17	-31.59
	Filterer	Brachycentrus	11.82%	4.16	-31.86
	Filterer	Prosimulium	2.48%	5.83	-26.90
		% total biomass	92.27%		
		Calculated isotope ratios for whole stream		3.94	-29.33
L.Pass-October-1988	Coll./Gath.	Ephemerella	4.76%	4.35	-29.44
	Coll./Gath.	Chironomidae	6.35%	2.90	-26.94
	Scraper	Glossosoma	2.38%	5.43	-30.01
	Predator	Drunella	2.78%	4.74	-29.12
	Predator	Isoperla	1.19%	5.93	-28.07
	Shredder	Hydatophylax	26.98%	2.78	-26.87
	Shredder	Ecclisomyia	0.40%	2.97	-26.81
	Filterer	Brachycentrus	48.41%	5.58	-29.98
		% total biomass	93.25%		
		Calculated isotope ratios for whole stream		4.49	-28.78
L.Troublesome-April-1988	Coll./Gath.	Baetis	15.72%	2.08	-29.20
	Coll./Gath.	Ephemerella	22.67%	1.76	-27.59
	Scraper	Heptageniidae	1.82%	1.40	-29.36
	Predator	Drunella	13.67%	1.39	-28.16
	Predator	Rhyacophila	9.11%	3.99	-26.40
	Shredder	Onocosmoecus	18.91%	0.33	-27.20
	Filterer	Prosimulium	2.16%	1.32	-28.51
	Filterer	Brachycentrus	4.21%	2.87	-28.38
		% total biomass	88.27%		
		Calculated isotope ratios for whole stream		1.72	-27.86
L.Troublesome-June-1988	Coll./Gath.	Baetis	8.12%	0.17	-26.62
	Coll./Gath.	Ephemerella	18.17%	1.02	-28.13
	Scraper	Heptageniidae	10.83%	0.36	-27.73
	Predator	Drunella	40.27%	2.05	-27.09
	Predator	Plumiperla	3.55%	3.70	-26.18
	Filterer	Prosimulium	4.67%	1.07	-27.40
	Filterer	Brachycentrus	7.61%	2.03	-27.43
		% total biomass	93.22%		
		Calculated isotope ratios for whole stream		1.50	-27.33

L.Troublesome-August-1988	Coll./Gath.	Chironomidae	4.82%	0.83	-22.36
	Coll./Gath.	Psychoglypha	21.71%	-1.13	-26.64
	Scraper	Heptageniidae	15.03%	0.78	-27.94
	Scraper	Glossosoma	1.86%	0.58	-26.70
	Predator	Drunella	29.87%	0.93	-25.06
	Predator	Plumiperla	7.24%	2.72	-29.70
	Shredder	Ecclisomyia	2.41%	-1.24	-25.27
	Shredder	Zapada	1.48%	-0.11	-27.54
	Filterer	Prosimulium	2.23%	2.08	-24.29
	Filterer	Brachycentrus	8.91%	1.20	-26.82
		% total biomass	95.56%		
		Calculated isotope ratios for whole stream		0.54	-26.31
L.Troublesome-October-1988	Coll./Gath.	Ephemerella	7.83%	3.03	-27.16
	Coll./Gath.	Chironomidae	1.00%	0.85	-25.86
	Scraper	Heptageniidae	9.33%	3.29	-26.12
	Scraper	Glossosoma	0.17%	2.93	-24.71
	Predator	Drunella	19.33%	1.47	-23.49
	Predator	Isoperla	1.83%	3.17	-26.93
	Shredder	Ecclisomyia	20.33%	2.05	-27.63
	Shredder	Zapada	4.33%	1.67	-28.38
	Filterer	Brachycentrus	23.67%	4.03	-26.62
	Filterer	Arctopsyche	2.00%	5.62	-25.96
		% total biomass	89.82%		
		Calculated isotope ratios for whole stream		2.73	-26.24
U.Pass-April-1988	Coll./Gath.	Ephemerella	64.15%	2.78	-37.06
	Predator	Drunella	1.57%	2.00	-37.19
	Predator	Isoperla	2.83%	2.92	-40.19
	Filterer	Brachycentrus	25.03%	3.71	-34.84
		% total biomass	93.58%		
		Calculated isotope ratios for whole stream		3.02	-36.56
U.Pass-June-1988	Coll./Gath.	Baetis	4.33%	3.10	-37.37
	Coll./Gath.	Ephemerella	80.45%	1.13	-36.42
	Coll./Gath.	Psychoglypha	2.60%	1.06	-31.88
	Scraper	Heptageniidae	5.54%	1.12	-37.83
	Predator	Isoperla	0.35%	4.09	-36.29
	Filterer	Prosimulium	0.52%	2.54	-31.72
	Filterer	Brachycentrus	1.90%	3.09	-33.76
		% total biomass	95.69%		
		Calculated isotope ratios for whole stream		1.27	-36.34
U.Pass-August-1988	Coll./Gath.	Ephemerella	7.28%	2.17	-34.55
	Coll./Gath.	Psychoglypha	54.89%	3.13	-32.33
	Scraper	Heptageniidae	5.20%	1.02	-36.28
	Predator	Drunella	8.11%	2.26	-35.83
	Filterer	Prosimulium	18.50%	2.78	-31.53
	Filterer	Brachycentrus	3.33%	3.60	-32.03
		% total biomass	97.31%		
		Calculated isotope ratios for whole stream		2.82	-32.84
U.Pass-October-1988	Coll./Gath.	Ephemerella	22.07%	3.77	-35.73
	Coll./Gath.	Psychoglypha	11.17%	2.84	-31.40
	Scraper	Heptageniidae	4.36%	3.90	-38.24
	Scraper	Glossosoma	4.90%	3.52	-34.84
	Predator	Drunella	3.00%	2.62	-35.74
	Predator	Isoperla	1.09%	4.89	-32.22
	Shredder	Tipula	3.27%	3.24	-34.53
	Filterer	Brachycentrus	40.05%	4.23	-33.32
		% total biomass	89.91%		
		Calculated isotope ratios for whole stream		3.81	-34.11

U.Troublesome-April-1988	Coll./Gath.	Baetis	13.29%	1.60	-28.55
	Coll./Gath.	Ephemerella	6.33%	2.27	-27.35
	Scraper	Heptageniidae	6.33%	2.73	-28.29
	Predator	Drunella?	12.66%	2.74	-27.43
	Predator	Rhyacophila	2.53%	4.78	-25.16
	Shredder	Onocosmoecus	44.30%	0.67	-27.34
	Filterer	Prosimulium	2.53%	2.21	-27.04
	Filterer	Brachycentrus	6.33%	2.72	-26.93
		% total biomass	94.30%		
		Calculated isotope ratios for whole stream		1.61	-27.49
U.Troublesome-June-1988	Coll./Gath.	Ephemerella	8.35%	0.63	-27.67
	Coll./Gath.	Psychoglypha	10.35%	-1.87	-25.79
	Scraper	Heptageniidae	12.90%	-0.78	-30.81
	Predator	Drunella	6.07%	0.42	-28.33
	Predator	Rhyacophila	4.74%	2.88	-26.72
	Shredder	Zapada	0.57%	0.04	-27.50
	Shredder	Tipula	3.96%	-0.17	-27.14
	Filterer	Prosimulium	1.71%	1.68	-27.43
	Filterer	Brachycentrus	42.69%	2.80	-27.72
		% total biomass	91.34%		
		Calculated isotope ratios for whole stream		1.25	-27.89
U.Troublesome-August-1988	Coll./Gath.	Chironomidae	4.05%	1.86	-25.15
	Coll./Gath.	Psychoglypha	28.90%	-0.37	-25.90
	Scraper	Heptageniidae	5.78%	0.09	-29.42
	Predator	Drunella	13.29%	1.19	-27.89
	Predator	Rhyacophila	23.12%	3.16	-25.85
	Shredder	Ecclisomyia	3.47%	-1.79	-26.50
	Shredder	Zapada	8.67%	1.09	-26.53
	Filterer	Brachycentrus	1.16%	2.32	-26.92
	Filterer	Arctopsyche	2.89%	2.89	-26.09
		% total biomass	91.33%		
		Calculated isotope ratios for whole stream		1.10	-26.47
U.Troublesome-October-1988	Coll./Gath.	Ephemerella	2.89%	0.84	-27.38
	Scraper	Heptageniidae	2.89%	1.72	-29.25
	Scraper	Glossosoma	0.72%	-0.36	-27.59
	Predator	Drunella	1.44%	0.62	-27.88
	Predator	Rhyacophila	13.72%	3.06	-25.92
	Shredder	Ecclisomyia	2.17%	1.55	-26.55
	Shredder	Zapada	9.39%	1.23	-27.33
	Filterer	Brachycentrus	45.85%	2.70	-25.94
	Filterer	Arctopsyche	16.61%	3.81	-26.80
		% total biomass	95.68%		
		Calculated isotope ratios for whole stream		2.63	-26.42
L.Pass-April-1990	Coll./Gath.	Baetis	4.15%	3.84	-39.16
	Coll./Gath.	Ephemerella	29.93%	5.82	-31.09
	Scraper	Glossosoma	0.31%	2.51	-32.84
	Scraper	Heptagenia	1.43%	4.08	-32.66
	Predator	Drunella	42.01%	6.02	-34.69
	Predator	Rhyacophila	5.43%	6.22	-30.45
	Shredder	Doddsia	1.18%	2.51	-38.80
	Shredder	Ecclisomyia	7.74%	5.29	-30.37
	Filterer	Brachycentrus	3.16%	4.45	-31.05
		% total biomass	95.34%		
		Calculated isotope ratios for whole stream		5.68	-33.06

L.Pass-June-1990	Coll./Gath.	Baetis	3.66%	3.84	-33.91
	Coll./Gath.	Ephemerella	7.18%	1.24	-31.41
	Scraper	Ironodes	1.83%	3.12	-32.91
	Scraper	Cynigmula	8.03%	3.96	-31.82
	Predator	Drunella	43.52%	3.61	-32.92
	Predator	Plumiperla	14.92%	10.20	-24.99
	Shredder	Ecclisomyia	0.99%	2.36	-25.91
	Shredder	Tipula	1.41%	2.33	-29.59
	Filterer	Brachycentrus	7.61%	3.75	-32.75
	Filterer	Prosimulium	1.41%	4.51	-30.07
		% total biomass	90.56%		
		Calculated isotope ratios for whole stream		4.53	-31.25
L.Pass-August-1990	Coll./Gath.	Ephemerella	6.00%	1.79	-30.01
	Coll./Gath.	Chironomidae	1.00%	1.82	-30.64
	Coll./Gath.	Psychoglypha	2.00%	-1.34	-24.48
	Scraper	Glossosoma	3.00%	2.00	-32.14
	Scraper	Ironodes	6.00%	2.63	-33.19
	Predator	Drunella	48.00%	3.01	-30.64
	Predator	Plumiperla	6.00%	4.27	-29.00
	Filterer	Prosimulium	3.00%	3.62	-30.92
	Filterer	Brachycentrus	13.00%	1.52	-32.05
		% total biomass	88.00%		
		Calculated isotope ratios for whole stream		2.64	-30.79
L.Pass-October-1990	Coll./Gath.	Ephemerella	21.95%	4.62	-30.53
	Scraper	Glossosoma	0.75%	2.43	-34.99
	Scraper	Heptagenia	0.75%	5.20	-28.16
	Predator	Drunella	43.89%	6.75	-31.29
	Predator	Rhyacophila	1.87%	5.09	-29.18
	Shredder	Zapada	3.62%	3.55	-29.32
	Shredder	Tipula	1.12%	4.08	-26.84
	Filterer	Brachycentrus	17.08%	4.23	-31.84
		% total biomass	91.03%		
		Calculated isotope ratios for whole stream		5.52	-33.06
L.Troublesome-April-1990	Coll./Gath.	Baetis	6.49%	4.64	-30.29
	Coll./Gath.	Ephemerella	26.91%	4.93	-27.83
	Scraper	Ironodes	8.72%	3.77	-29.05
	Scraper	Glossosoma	0.92%	2.37	-24.31
	Predator	Drunella	21.33%	4.80	-28.12
	Predator	Rhyacophila	4.88%	4.75	-26.28
	Shredder	Zapada	12.43%	5.42	-26.92
	Shredder	Doddsia	5.13%	2.11	-30.40
	Shredder	Ecclisomyia	0.66%	3.84	-27.60
	Filterer	Arctopsyche	1.32%	4.83	-26.66
	Filterer	Brachycentrus	0.62%	4.73	-26.41
		% total biomass	89.41%		
		Calculated isotope ratios for whole stream		4.62	-28.07
L.Troublesome-June-1990	Coll./Gath.	Baetis	0.50%	2.20	-30.36
	Coll./Gath.	Ephemerella	0.60%	0.83	-29.16
	Scraper	Ironodes	17.00%	2.66	-32.07
	Scraper	Cynigmula	10.00%	3.19	-30.04
	Predator	Drunella	42.00%	3.15	-31.72
	Predator	Plumiperla	16.00%	9.55	-24.58
	Filterer	Arctopsyche	1.00%	7.23	-25.89
	Filterer	Brachycentrus	1.00%	3.81	-28.95
		biomass represeted	88.10%		
		Calculated isotope ratios for whole stream		4.25	-30.18

L.Troublesome-August-1990	Coll./Gath.	Ephemerella	7.67%	2.48	-24.58
	Coll./Gath.	Chironomidae	12.28%	4.34	-25.44
	Scraper	Glossosoma	5.49%	3.22	-25.12
	Scraper	Ironodes	12.46%	4.36	-28.97
	Predator	Drunella	31.62%	3.06	-26.83
	Predator	Plumiperla	7.84%	4.42	-25.98
	Shredder	Zapada	1.13%	2.47	-28.67
	Shredder	Ecclisomyia	0.52%	1.18	-25.64
	Filterer	Arctopsyche	1.22%	3.75	-25.21
	Filterer	Brachycentrus	4.18%	1.42	-27.39
		% total biomass	84.41%		
		Calculated isotope ratios for whole stream		3.43	-26.57
L.Troublesome-October-1990	Coll./Gath.	Ephemerella	7.62%	2.80	-27.24
	Coll./Gath.	Chironomidae	0.91%	3.70	-28.74
	Scraper	Glossosoma	1.83%	4.29	-27.55
	Scraper	Ironodes	5.18%	2.27	-28.94
	Predator	Drunella	32.62%	4.14	-26.44
	Predator	Rhyacophila	6.40%	4.89	-26.46
	Shredder	Zapada	10.06%	1.65	-28.16
	Filterer	Arctopsyche	10.37%	6.20	-24.70
	Filterer	Brachycentrus	18.90%	3.49	-26.41
		% total biomass	93.69%		
		Calculated isotope ratios for whole stream		3.81	-26.67
U.Pass-April-1990	Coll./Gath.	Ephemerella	43.28%	1.88	-41.74
	Coll./Gath.	Chironomidae	10.27%	1.94	-38.91
	Scraper	Glossosoma	3.78%	2.45	-34.58
	Scraper	Heptagenia	1.21%	1.23	-44.56
	Predator	Drunella	5.66%	2.66	-38.00
	Predator	Isoperla	4.91%	4.56	-37.39
	Shredder	Doddsia	1.51%	-1.28	-41.82
	Shredder	Tipula	5.36%	4.29	-25.98
	Filterer	Brachycentrus	13.75%	2.48	-25.83
	Filterer	Prosimulium	0.91%	-1.02	-44.27
		% total biomass	90.64%		
		Calculated isotope ratios for whole stream		2.25	-37.37
U.Pass-June-1990	Coll./Gath.	Baetis	13.00%	3.24	-39.26
	Coll./Gath.	Ephemerella	17.95%	0.40	-36.63
	Scraper	Glossosoma	0.92%	4.48	-36.80
	Predator	Drunella	9.20%	1.27	-34.24
	Predator	isoperla	3.11%	3.62	-35.78
	Shredder	Zapada	1.80%	0.84	-26.86
	Filterer	Prosimulium	32.05%	3.09	-31.87
		% total biomass	78.03%		
		Calculated isotope ratios for whole stream		2.27	-34.57
U.Pass-August-1990	Coll./Gath.	Ephemerella	25.31%	1.31	-33.65
	Coll./Gath.	Psychoglypha	24.22%	-0.35	-30.62
	Scraper	Glossosoma	1.86%	1.69	-33.05
	Scraper	Apatania	3.42%	0.58	-30.03
	Predator	Drunella	1.24%	1.88	-35.70
	Predator	Plumiperla	0.93%	4.11	-32.32
	Shredder	Tipula	0.47%	1.26	-36.08
	Filterer	Brachycentrus	31.52%	1.27	-34.01
	Filterer	Prosimulium	2.17%	3.08	-32.33
		% total biomass	91.14%		
		Calculated isotope ratios for whole stream		1.10	-32.82

U.Pass-October-1990	Coll./Gath.	Ephemerella	18.54%	3.54	-33.93
	Coll./Gath.	Chironomidae	1.67%	3.89	-31.25
	Scraper	Glossosoma	3.71%	3.63	-36.56
	Scraper	Apatania	3.61%	2.44	-35.61
	Predator	Drunella	2.76%	3.13	-36.75
	Predator	Isoperla	0.74%	5.49	-32.45
	Shredder	Zapada	0.19%	1.63	-32.83
	Filterer	Brachycentrus	59.13%	4.83	-31.97
		% total biomass	90.35%		
		Calculated isotope ratios for whole stream		4.35	-32.84
U.Troublesome-April-1990	Coll./Gath.	Baetis	1.27%	3.17	-29.55
	Coll./Gath.	Ephemerella	14.32%	2.51	-26.67
	Scraper	Ironodes	8.18%	3.56	-28.69
	Predator	Rhyacophila	5.92%	3.80	-26.33
	Predator	Drunella	1.48%	2.40	-28.18
	Shredder	Zapada	9.73%	3.28	-26.83
	Shredder	Ecclisomyia	5.08%	1.99	-27.51
	Filterer	Arctopsyche	14.25%	3.59	-26.35
	Filterer	Brachycentrus	28.70%	3.83	-33.20
		% total biomass	88.93%		
		Calculated isotope ratios for whole stream		3.35	-29.02
U.Troublesome-June-1990	Coll./Gath.	Baetis	4.66%	3.02	-29.43
	Coll./Gath.	Ephemerella	16.64%	-0.03	-29.99
	Scraper	Ironodes	9.48%	3.95	-30.07
	Scraper	Cynigmula	6.32%	3.59	-28.02
	Predator	Drunella	3.00%	2.34	-29.95
	Predator	Rhyacophila	4.33%	3.52	-26.96
	Shredder	Ecclisomyia	1.83%	1.08	-26.76
	Filterer	Arctopsyche	7.32%	3.90	-26.66
	Filterer	Brachycentrus	35.61%	2.40	-27.12
		% total biomass	89.19%		
		Calculated isotope ratios for whole stream		2.38	-28.20
U.Troublesome-August-1990	Coll./Gath.	Chironomidae	1.49%	0.34	-22.90
	Coll./Gath.	Psychoglypha	6.24%	-1.38	-24.22
	Scraper	Glossosoma	1.09%	-0.21	-33.54
	Scraper	Ironodes	1.98%	0.22	-30.09
	Predator	Rhyacophila	6.44%	2.12	-26.35
	Predator	Drunella	2.38%	-0.28	-26.83
	Shredder	Zapada	3.07%	0.69	-27.32
	Shredder	Ecclisomyia	1.09%	-1.47	-24.94
	Filterer	Arctopsyche	32.77%	2.90	-25.44
	Filterer	Brachycentrus	40.00%	-0.09	-24.62
		% total biomass	96.55%		
		Calculated isotope ratios for whole stream		1.01	-25.32
U.Troublesome-October-1990	Coll./Gath.	Ephemerella	7.03%	-0.07	-26.93
	Coll./Gath.	Chironomidae	0.66%	3.06	-25.23
	Scraper	Glossosoma	1.23%	0.63	-26.96
	Scraper	Ironodes	11.11%	1.58	-28.71
	Predator	Drunella	2.28%	0.29	-27.19
	Predator	Rhyacophila	8.64%	2.85	-24.99
	Shredder	Zapada	18.42%	0.87	-28.13
	Shredder	Ecclisomyia	0.95%	-0.31	-28.73
	Filterer	Arctopsyche	17.95%	3.52	-25.61
	Filterer	Brachycentrus	26.21%	1.63	-25.52
		% total biomass	94.48%		
		Calculated isotope ratios for whole stream		1.77	-26.57

APPENDIX C- Other Stable Isotope Data

CREEK	Biota of Interest	SALMON?	AVE ∂ N	AVE. ∂ C
Byers Ck 5/93	Amphipod	YES	5.95	-28.91
Byers Ck 5/93	*Arcynopteryx*	YES	6.23	-34.32
Byers Ck 5/93	*Limnephilius*	YES	3.57	-29.53
Byers Ck 5/93	*Onocosmoecus*	YES	4.3	-29.79
Fish Ck Paxson-6/93	*Arctopsyche*	YES	6.05	-30.17
Fish Ck Paxson-6/93	*Chironomidae*	YES	3.84	-26.98
Fish Ck Paxson-6/93	*Drunella*	YES	6.34	-34.69
Fish Ck Paxson-6/93	*Ecclisomyia*	YES	7.95	-32.49
Fish Ck Paxson-6/93	*Epeorus*	YES	5.2	-35.4
Fish Ck Paxson-6/93	*Ephemerella*	YES	5.28	-31.59
Fish Ck Paxson-6/93	*Limnephilius*	YES	7.05	-29.62
Fish Ck Paxson-6/93	*Onocosmoecus*	YES	6.4	-27.82
Fish Ck Paxson-6/93	*Prosimulium*	YES	4.73	-34.18
Rock Ck Paxson-5/93	*Arctopsyche*	NO	3.13	-31.81
Rock Ck Paxson-5/93	*Drunella*	NO	1.82	-38.71
Rock Ck Paxson-5/93	*Ecclisomyia*	NO	3.15	-37.86
Rock Ck Paxson-5/93	*Epeorus*	NO	1.83	-38.13
Rock Ck Paxson-5/93	*Ephemerella*	NO	1.3	-35.15
Rock Ck Paxson-5/93	*Plumiperla*	NO	4.44	-33.66
Rock Ck Paxson-5/93	Sculpin	NO	4.82	-32.69
Summit Ck Paxson-6/93	*Arctopsyche*	YES	7.26	-31.76
Summit Ck Paxson-7/91	*Arctopsyche*	YES	4.07	-27.77
Summit Ck Paxson-6/93	*Brachycentrus*	YES	5.8	-29.63
Summit Ck Paxson-6/93	*Chironomidae*	YES	6.26	-26.19
Summit Ck Paxson-7/91	*Chironomidae*	YES	3.9	-22.57
Summit Ck Paxson-6/93	*Drunella*	YES	6.33	-35.11
Summit Ck Paxson-6/93	*Ecclisomyia*	YES	6.2	-33.19
Summit Ck Paxson-6/93	*Ephemerella*	YES	6.56	-30.11
Summit Ck Paxson-7/91	*Ephemerella*	YES	3.4	-27.84
Summit Ck Paxson-6/93	*Isoperla*	YES	4.64	-32.21
Summit Ck Paxson-6/93	*Limnephilius*	YES	5.8	-29.35
Summit Ck Paxson-6/93	*Onocosmoecus*	YES	6.65	-31.26
Summit Ck Paxson-6/93	*Rhyacophila*	YES	7.33	-27.12
Summit Ck Paxson-6/93	*Tipula*	YES	3.1	-22.79
Summit Ck Cantwell-6/93	*Brachycentrus*	NO	5	-32.18
Summit Ck Cantwell-6/93	*Ephemerella*	NO	3.67	-36.09
Summit Ck Cantwell-6/93	*Onocosmoecus*	NO	5.03	-30.11
Summit Ck Cantwell-6/93	*Tipula*	NO	3.66	-30.32
Clear Ck Clear 5/93	*Ameletus*	YES	3.22	-40.75
ClearCk Clear 5/93	*Baetis*	YES	4.08	-40.15
ClearCk Clear 11/93	*Brachycentrus*	YES	4.39	-38.73
ClearCk Clear 11/93	*Chironomidae*	YES	3.62	-38.19

ClearCk Clear 11/93	Coho fry	YES	9.15	-32.9
ClearCk Clear 5/93	*Drunella*	YES	4.94	-39.55
ClearCk Clear 11/93	*Ephemerella*	YES	4.86	-35.6
ClearCk Clear 11/93	*Isoperla*	YES	7.71	-34.66
ClearCk Clear 5/93	*Isoperla*	YES	7.29	-36.59
ClearCk Clear 11/93	*Rhyacophila*	YES	5.51	-37.51
ClearCk Clear 11/93	*Zapada*	YES	4.12	-34.56
Fish Ck Talkeetna5/93	*Amphipod*	YES	6.32	-31.76
Fish Ck Talkeetna5/93	*Arctopsyche*	YES	7.29	-36.68
Fish Ck Talkeetna5/93	Coho fry	YES	14.16	-22.44
Fish Ck Talkeetna5/93	*Ecclisomyia*	YES	6.56	-34.27
Fish Ck Talkeetna5/93	*Ephemerella*	YES	5.11	-36.88
Fish Ck Talkeetna5/93	Leech	YES	7.74	-30.44
Fish Ck Talkeetna5/93	*Limnephilius*	YES	5.39	-33.23
Fish Ck Talkeetna5/93	*Onocosmoecus*	YES	5.39	-36.99
Fish Ck Talkeetna5/93	*Plumiperla*	YES	12.32	-26.73
Fish Ck Talkeetna5/93	*Tipula*	YES	4.52	-29.3
Octopus Ck Paxson 5/93	*Tipula*	NO	1.66	-27.48
Tangle R Paxson 6/93	*Brachycentrus*	NO	5.1	-32.27
Tangle R Paxson 6/93	*Ecclisomyia*	NO	10.27	-37.06
Tangle R Paxson 6/93	*Ephemerella*	NO	5.22	-32.97
Tangle R Paxson 6/93	*Isoperla*	NO	6.78	-37.2
Tangle R Paxson 6/93	*Isoperla-emerging*	NO	7.06	-34.46
Tangle R Paxson 6/93	*Onocosmoecus*	NO	9.25	-40.06
Tangle R Paxson 6/93	*Tipula*	NO	3.48	-28.95
Mud Ck Paxson 6/93	*Isoperla*	NO	5.87	-38.73
Mud Ck Paxson 6/93	*Onocosmoecus*	NO	1.25	-31.73
Mud Ck Paxson 6/93	*Tipula*	NO	2.1	-26.27
Mud Ck Paxson 6/93	*Ecclisomyia*	NO	4.12	-33.8
Mud Ck Paxson 6/93	*Chironomidae*	NO	2.67	-34.64
Fielding Ck Paxson 6/93	*Baetis*	NO	4.02	-37.05
Fielding Ck Paxson 6/93	*Ecclisomyia*	NO	5.09	-32.15
Fielding Ck Paxson 6/93	*Ephemerella*	NO	2.9	-33.65
Fielding Ck Paxson 6/93	*Isoperla*	NO	6.3	-34.46
Fielding Ck Paxson 6/93	*Onocosmoecus*	NO	4.47	-35
Fielding Ck Paxson 6/93	*Prosimulium*	NO	4.63	-38.01
Fielding Ck Paxson 6/93	*Tipula*	NO	2.79	-29.64
Landmark Ck Paxson 6/93	*Brachycentrus*	NO	2.43	-27.26
Landmark Ck Paxson 6/93	*Epeorus*	NO	2.16	-29.74
Landmark Ck Paxson 6/93	*Ephemerella*	NO	1.22	-27.95
Landmark Ck Paxson 6/93	*Isoperla*	NO	4.22	-27.75
Landmark Ck Paxson 6/93	*Tipula*	NO	0.54	-22.85

Big Lk Ck Wasilla 6/93	*Limnephilius*	YES	9	-29.62
Big Lk Ck Wasilla 6/93	*Onocosmoecus*	YES	9.72	-31.26
Nancy Lk Willow 6/93	Amphipod	YES	6.97	-34.02
Nancy Lk Willow 6/93	Leech	YES	9.39	-31.19
Nancy Lk Willow 6/93	Pelecypoda	YES	7.47	-35.46
Clear Water R Delta 11/90	*Ecclisomyia-on fish*	YES	5.38	-37.78
Clear Water R Delta 11/90	*Onocosmoecus-on fish*	YES	4.73	-36.6
Clear Water R Delta 11/90	*Prosimulium-on fish*	YES	5.2	-35.31
Clear Water R Delta 11/90	*Zapada-on fish*	YES	4.86	-36.61
Byers Ck 10/87	*Arctopsyche*	YES	5.68	-28.48
Chatanika R 9/93	*Arctopsyche*	YES	5.85	-33.85
Tanana R FBKS-9/92	*Arctopsyche*	YES	4.35	-30.22
Lower Pass Ck 8/88	*Calliphoridae-on fish*	YES	16.05	-18.76
Horshoe Ck 9/88	*Ecclisomyia-on fish*	YES	5.81	-33.21
Horshoe Ck 9/88	*Ecclisomyia-on fish*	YES	6.42	-30.18
Ballaine Lk FBKS 9/88	*Nemataulius*	NO	5.41	-27.55
Kaltag R 8/92	*Psychoglypha*	YES	1.89	-28.21
Lower Pass Ck 8/90	*Psychoglypha-on fish*	YES	7.01	-26.37
Lower Pass Ck 8/90	*Psychoglypha-on fish*	YES	5.89	-26.8
Byers Ck 8/88	*Psychoglypha-on fish*	YES	3.03	-25.72
Tonzona R 3/88	*Zapada/ Heptageniidae*	NO	0.77	-35.26
Byers Ck 5/88	American Dipper	YES	8.38	-25.6
Honolululu Ck 5/88	American Dipper	YES	6.49	-31.42
Honolululu Ck 5/88	American Dipper	YES	6.26	-31.48
Horseshoe Ck 10/88	American Dipper	YES	5.69	-27.83
Horseshoe Ck 10/88	American Dipper	YES	5.77	-28.29
L Troublesome Ck 10/88	American Dipper	YES	4.91	-26.59
L Troublesome Ck 10/88	American Dipper	YES	8.3	-26.84
L Troublesome Ck 10/88	American Dipper	YES	8.62	-23.74
Tonzona R 3/88	American Dipper	NO	4.54	-32.36
Tonzona R 3/88	American Dipper	NO	4.15	-34.3
Byers Ck 8/88	Aufwuchs	YES	5	-22.42
Honolulu Ck 5/88	Aufwuchs	YES	-0.05	-32.37
MF Chulitna R 3/88	Aufwuchs	YES	0.7	-43.98
Byers Ck 7/90	Aufwuchs	YES	2.89	-22.26
Honolulu Ck 8/90	Aufwuchs	YES	0.32	-30.17
U Pass Ck 8/90	Aufwuchs	NO	-0.14	-25.82
U Pass Ck 4/90	Aufwuchs	NO	3.26	-36.81
Smt.Ck Paxson 6/93	Aufwuchs	YES	3.62	-31.93

EF Chulitna R-7/93	Aufwuchs	YES	-0.13	-34.28
L Pass Ck-7/93	Aufwuchs	YES	2.25	-27.13
L Troublesome Ck-7/93	Aufwuchs	YES	0.46	-25.06
MF Chulitna R-7/93	Aufwuchs-slough	YES	2.67	-36.04
MF Chulitna R-7/93	Aufwuchs	YES	1.81	-32.39
Byers Ck 8/93	Aufwuchs	YES	5.79	-19.88
Byers Ck 8/93	Aufwuchs-below fish	YES	6.56	-21.73
Honolulu Ck 8/93	Aufwuchs	YES	0.67	-30.26
Horseshoe Ck-8/93	Aufwuchs-spring	YES	0.26	-37.92
Horseshoe Ck-8/93	Aufwuchs-below fish	YES	2.13	-33.6
L Pass Ck-8/93	Aufwuchs-below fish	YES	4.47	-24.45
L Pass Ck-8/93	Aufwuchs	YES	2.78	-27.74
L Troublesome Ck-8/93	Aufwuchs	YES	2.14	-17.81
MF Chulitna R-8/93	Aufwuchs-below fish	YES	7.61	-12.69
MF Chulitna R-8/93	Aufwuchs	YES	2.48	-22.49
U Pass Ck-8/93	Aufwuchs	NO	2.55	-29.18
Byers Ck 10/93	Aufwuchs	YES	3.86	-
Honolulu Ck 10/93	Aufwuchs	YES	1.99	-
L Pass Ck-10/93	Aufwuchs	YES	2.22	-11.91
L Troublesome Ck-10/93	Aufwuchs-spring	YES	1.1	-
MF Chulitna R-10/93	Aufwuchs	YES	1.7	-28.91
U Pass Ck-10/93	Aufwuchs	NO	2.12	-
U Troublesome Ck-10/93	Aufwuchs	NO	-0.26	-
Byers Ck 10/87	Heterotroph	YES	2.04	-22.97
Byers Ck 10/90	Heterotroph	YES	5.34	-20.05
Byers Ck 3/88	Heterotroph	YES	7.31	-24.98
Byers Ck 5/88	Heterotroph	YES	4.64	-22.35
Byers Ck 7/88	Heterotroph	YES	-0.04	-17.12
Byers Ck 8/88	Heterotroph	YES	2.04	-20.26
Byers Ck 8/90	Heterotroph	YES	10.25	-19.06
Byers Ck source 3/88	Heterotroph	YES	4.14	-23.4
EF Chulitna R 8/90	Heterotroph	YES	0.9	-20.83
MF Chulitna R 8/93	Heterotroph-on fish	YES	12.11	-23.05
Smt.Ck Paxson 6/93	Heterotroph	YES	2.57	-22.65
Wonder Lk Ck 6/93	Heterotroph	NO	0.45	-20.32
Byers Ck 10/88	MOSS	YES	6.56	-30.87
Byers Ck 3/88	MOSS	YES	5.5	-34.16
Byers Ck 5/88	MOSS	YES	5.15	-32.06
Honolulu Ck 7/93	MOSS	YES	-1.08	-32.61
U Troublesome Ck 7/93	MOSS	NO	0.52	-29.56
U Troublesome Ck8/90	MOSS	NO	0.12	-26.33
U Troublesome Ck 9/88	MOSS	NO	-1.63	-26.85
Byers Ck 3/88	Potamageon	YES	4.52	-30.12

Horseshoe Ck 10/93	Potamageon	YES	0.61	-31.22
Byers Ck 10/93	Birch	YES	-1.96	-28.18
L Pass Ck10/93	Birch	YES	-1.73	-27.92
L Troublesome Ck 10/93	Birch	YES	-1.61	-29.68
U Pass Ck/10/93	Grass	NO	1.49	-28.51
Byers Ck 10/93	Poplar	YES	-2.51	-27.78
EF Chulitna R 10/93	Poplar	YES	-9.99	-29.41
Honolulu Ck 10/93	Poplar	YES	-2.11	-28.4
Horseshoe Ck 10/93	Poplar	YES	-3.39	-27.93
L Pass Ck 10/93	Poplar	YES	-2.25	-28.11
L Troublesome Ck 10/93	Poplar	YES	-1.24	-28.48
MF Chulitna R 10/93	Poplar	YES	-7.28	-29.41
U Troublesome Ck 10/93	Poplar	NO	-2.76	-28.03
Byers Ck 10/93	Willow	YES	-1.35	-29.24
EF Chulitna R 10/93	Willow	YES	-3.43	-28.18
Honolulu Ck 10/93	Willow	YES	-1.77	-28.11
Horseshoe Ck 10/93	Willow	YES	-0.99	-27.96
L Pass Ck 10/93	Willow	YES	-1.24	-28.56
L Troublesome Ck 10/93	Willow	YES	-2.82	-28.36
MF Chulitna R 10/93	Willow	YES	-3.06	-27.66
U Pass Ck 10/93	Willow	NO	-1.5	-28.26
U Troublesome Ck 10/93	Willow	NO	-2.93	-28.56
Byers Ck 10/93	Alder	YES	-1.65	-28.85
EF Chulitna R 10/93	Alder	YES	-1.46	-28.51
Honolulu Ck 10/93	Alder	YES	-1.61	-26.64
L Pass Ck 10/93	Alder	YES	-1.74	-28.38
L Troublesome Ck 10/93	Alder	YES	-2.73	-27.08
MF Chulitna R 10/93	Alder	YES	-1.75	-27.09
U Troublesome Ck 10/93	Alder	NO	-1.68	-27.16
Byers Ck10/87	Sculpin-> one year	YES	9.51	-25.56
Byers Ck10/87	Sculpin-Young of year	YES	9.54	-25.27
Byers Ck10/87	Sculpin-One year	YES	9.34	-26.05
Byers Ck 5/88	Sculpin	YES	10.05	-25.86
Honolulu Ck 5/88	Sculpin	YES	4.75	-28.34
Honolulu Ck 5/88	Sculpin	YES	4.74	-28.4
L Pass Ck-5/88	Sculpin	YES	5.64	-28.56
L Troublesome Ck-5/88	Sculpin	YES	6.38	-24.68
U Pass Ck 5/88	Sculpin	NO	7.52	-35.03
Byers Ck 7/88	Sculpin	YES	8.29	-30.95
Honolulu Ck 7/88	Sculpin	YES	6.88	-29.93
L Pass Ck-7/88	Sculpin	YES	9.02	-26.69
L Troublesome Ck-7/88	Sculpin	YES	6.6	-27.14

U Pass Ck-7/88	Sculpin	NO	8.83	-23.6
U Troublesome Ck-7/88	Sculpin	NO	4.65	-25.62
Byers Ck10/88	Sculpin	YES	9.84	-26.66
Honolulu Ck10/88	Sculpin	YES	8.83	-34.17
L Pass Ck 10/88	Sculpin	YES	5.24	-27.58
L Pass Ck 9/88	Sculpin	YES	10.68	-27.43
L Troublesome Ck10/88	Sculpin	YES	6.18	-24.88
U Pass Ck 10/88	Sculpin	NO	7.06	-35.24
Byers Ck 4/90	Sculpin	YES	8.79	-25.34
EF Chulitna R 5/90	Sculpin	YES	5.36	-30
Honolulu Ck 5/90	Sculpin	YES	5.08	-23.01
L Troublesome Ck 5/90	Sculpin	YES	6.31	-23.57
MF Chulitna R 5/90	Sculpin	YES	7.01	-30.36
U Pass Ck 4/90	Sculpin	YES	7.18	-33.99
U Troublesome Ck 4/90	Sculpin	NO	5.31	-24.71
Byers Ck 8/90	Sculpin	YES	8.55	-24.33
EF Chulitna R 7/90	Sculpin	YES	5.9	-29.43
Honolulu Ck 7/90	Sculpin	YES	4.84	-27.91
L Pass Ck 7/90	Sculpin	YES	7.52	-30.74
L Troublesome Ck 7/90	Sculpin	YES	7.2	-25.96
MF Chulitna R 7/90	Sculpin	YES	6.03	-32.73
U Pass Ck 8/90	Sculpin	NO	6.71	-32.06
U Troublesome Ck 7/90	Sculpin	NO	5.36	-24.31
Byers Ck 10/90	Sculpin	YES	9.47	-24.01
EF Chulitna R 10/90	Sculpin	YES	5.65	-29.07
Honolulu Ck 10/90	Sculpin	YES	4.2	-27.84
L Pass Ck 10/90	Sculpin	YES	7.93	-31.43
L Troublesome Ck 10/90	Sculpin	YES	5.6	-22.37
MF Chulitna R 10/90	Sculpin	YES	6.46	-31.97
U Pass Ck 10/90	Sculpin	NO	7.74	-33.39
U Troublesome Ck 10/90	Sculpin	NO	7.62	-24.84
Summit Ck Cantwell 5/93	Sculpin	NO	6.71	-29.99
Fish Ck Talkeetna 5/93	Sculpin	YES	8.3	-34.98
Octopus Lk Cantwell 6/93	Sculpin	NO	7.22	-26.96
Fielding Lk Ck 6/93	Sculpin	NO	6.01	-31.87
Clear Ck Clear11/93	Sculpin	YES	7.9	-36.96
Clear Ck Clear11/93	Sculpin-Young of year	YES	8.07	-36.4
Crosswind Lk	Lake Trout	YES	12.16	-25.53
Crosswind Lk	Lake Trout	YES	12.11	-25.9
Crosswind Lk	Lake Trout	YES	11.96	-26.23
Crosswind Lk	Lake Trout	YES	13.51	-29.21
Summit Lk Paxson	Lake Trout	YES	15.11	-31.78
Summit Lk Paxson	Lake Trout	YES	14.47	-30.91
Summit Lk Paxson	Lake Trout	YES	14.41	-30.86

Summit Lk Paxson	Lake Trout	YES	14.68	-30.84
Paxson Lk Paxson	Lake Trout	YES	14.77	-32.62
Paxson Lk Paxson	Lake Trout	YES	14.67	-32.67
Paxson Lk Paxson	Lake Trout	YES	14.46	-26.94
Byers Lk	Lake Trout	YES	12	-17.77
Byers Lk	Lake Trout	YES	13.23	-33.92
Byers Lk	Lake Trout	YES	12.07	-33.07
7 mi Lk Ck 6/93	Lake Trout	NO	8.89	-32.49
7 mi Lk Ck 6/93	Lake Trout	NO	8.82	-34.28
7 mi Lk Ck 6/93	Lake Trout	NO	9.25	-33.07
7 mi Lk Ck 6/93	Lake Trout	NO	9.26	-30.29
Crazy Lk 7/93	Lake Trout	NO	8.59	-27.81
Crazy Lk 7/93	Lake Trout	NO	10.93	-26.29
Crazy Lk 7/93	Lake Trout	NO	10.95	-23.94
Crazy Lk 7/93	Lake Trout	NO	9.83	-27.32
Dickey Lk 6/93	Lake Trout	NO	12.6	-25.99
Harding Lk 7/92	Lake Trout	NO	16.03	-23.61
Harding Lk 7/92	Lake Trout	NO	14.67	-26.33
Lake Louise 7/92	Lake Trout	NO	13.09	-27.55
Lake Louise 7/92	Lake Trout	NO	11.76	-25.68
Lake Louise 7/92	Lake Trout	NO	12.53	-26.48
Lake Louise 7/92	Lake Trout	NO	12.64	-26.83
Tangle Lk 6/93	Lake Trout	NO	14.08	-31.48
Wonder Lk 6/91	Lake Trout	NO	15.62	-33.61
Wonder Lk 6/93	Lake Trout-gut contents	NO	4.81	-30.13
Wonder Lk 6/93	Lake Trout-gut contents	NO	2.8	-27.23
Wonder Lk 6/93	Lake Trout-gut contents	NO	3.22	-25.96
Wonder Lk 6/93	Lake Trout	NO	11.73	-29.1
Wonder Lk 6/93	Lake Trout	NO	10.92	-28.62
Wonder Lk 6/93	Lake Trout	NO	11.89	-29.14
Wonder Lk 6/93	Lake Trout	NO	10.94	-27.84
Indiana Lake 7/92	Lake Trout	NO	11.13	-23.83
Indiana Lake 7/92	Lake Trout	NO	11.57	-23.79
Indiana Lake 7/92	Lake Trout	NO	12.13	-27.96
Indiana Lake 7/92	Lake Trout	NO	11.26	-23.9
Summit Lk Paxson 7/92	Burbot	YES	14.68	-29.36
Summit Lk Paxson 7/91	Burbot	YES	14.58	-29.62

Summit Lk Paxson 7/91	Burbot	YES	14.49	-29.54
Paxson Lk 7/92	Burbot	YES	12.03	-26.16
Paxson Lk 7/92	Burbot	YES	14.77	-30.08
Paxson Lk 7/92	Burbot	YES	11.96	-25.84
Byers Ck 3/88	Burbot	YES	11.9	-28.95
Chena R 4/93	Burbot	YES	9.87	-28.47
Chena R 4/93	Burbot	YES	10.34	-28.31
ST.Ann Lk 7/88	Burbot	NO	12.14	-30.46
ST.Ann Lk 7/88	Burbot	NO	12.04	-30.23
ST.Ann Lk 7/88	Burbot	NO	11.69	-29.7
Lake Louise 7/92	Burbot	NO	12.42	-28.29
Lake Louise 7/92	Burbot	NO	10.57	-25.24
Lake Louise 7/92	Burbot	NO	9.83	-23.34
Lake Louise 7/92	Burbot	NO	12.8	-27.95
Lake Susitna 7/92	Burbot	NO	13.72	-27.31
Lake Susitna 7/92	Burbot	NO	13.36	-27.26
Moose Lk Paxson7/92	Burbot	NO	13.43	-26.49
Moose Lk Paxson7/92	Burbot	NO	8.35	-22.75
Moose Lk Paxson7/92	Burbot	NO	9.17	-23
L. Pass Ck 8/90	King salmon	YES	14.53	-18.35
L. Pass Ck 8/90	King salmon	YES	14.69	-19.43
L. Pass Ck 8/90	King salmon	YES	14.64	-17.82
L. Pass Ck 8/90	King salmon	YES	14.49	-18.49
L. Troublesome Ck 8/90	King salmon	YES	14.25	-17.74
L. Troublesome Ck 8/90	King salmon	YES	14.13	-19.35
MF Chulitna R 8/93	King salmon	YES	15.55	-19.08
MF Chulitna R 8/93	King salmon	YES	14.59	-20.08
MF Chulitna R 8/93	King salmon	YES	14.2	-22.07
MF Chulitna R 8/93	King salmon	YES	14.14	-20.97
Horseshoe Ck 8/93	King salmon	YES	15.39	-19.72
Byers Ck 9/90	Pink salmon	YES	12.85	-21.01
Byers Ck 9/90	Pink salmon	YES	11.45	-21.17
Byers Ck 9/90	Pink salmon	YES	11.54	-21.2
Byers Ck 9/90	Pink salmon	YES	11.85	-22.01
Byers Ck 9/90	Pink salmon	YES	11.59	-21.91
Byers Ck10/87	Coho	YES	10.44	-22.11
Byers Ck10/87	Coho	YES	12.04	-21.81
Byers Ck10/87	Coho	YES	12.55	-21.45

Tanana R 7/93	Chum salmon	YES	11.1	-20.08
Tanana R 7/93	Chum salmon	YES	11.48	-20.43
Tanana R 7/93	Chum salmon	YES	12.19	-20.06
Tanana R 7/93	Chum salmon	YES	11.25	-20.22
Tanana R Oct. I month old	Chum salmon	YES	12.32	-21.92
Tanana R Oct. I month old	Chum salmon	YES	12.02	-22.74
Tanana R Nov. I month old	Chum salmon	YES	14.15	-20.27
Tanana R Nov. I month old	Chum salmon	YES	12.98	-21.7
Tanana R Nov. I month old	Chum salmon	YES	13.05	-21.45
Tanana R Dec. I month old	Chum salmon	YES	13.80	-20.71
Tanana R Dec. I month old	Chum salmon	YES	13.14	-21.99
Tanana R Dec. I month old	Chum salmon	YES	12.89	-21.14
Tanana R Jan. I month old	Chum salmon	YES	14.01	-18.11
Byers Ck 10/87	Salmon eggs	YES	12.27	-22.76
Byers Ck 10/88	Salmon eggs	YES	12.45	-23.16
Honolulu Ck 10/88	Salmon eggs	YES	13.85	-22.02
L Pass Ck 10/88	Salmon eggs	YES	14.7	-21.72
L Troublesome Ck 10/88	Salmon eggs	YES	12.05	-22.97
Tangle R 6/93	Grayling-gut contents	NO	2.85	-29.71
Tangle R 6/93	Grayling	NO	8.53	-30.57
Tangle R 6/93	Grayling	NO	8.46	-31.15
Tangle R 6/93	Grayling	NO	8.15	-31.24
L Pass Ck 6/93	Grayling	YES	9.95	-25.73
L Pass Ck 6/93	Grayling	YES	11.27	-23.59
L Pass Ck 6/93	Grayling	YES	9.34	-27.7
L Pass Ck 8/93	Grayling	YES	9.25	-27.98
L Pass Ck 8/93	Grayling	YES	12.59	-24.06
L Pass Ck 8/93	Grayling	YES	12.03	-24.12
L Troublesome Ck 6/90	Rainbow trout	YES	13.82	-21.42
L Troublesome Ck 6/90	Rainbow trout	YES	14.5	-20.81
Byers Ck 8/90	Rainbow trout	YES	13.88	-22.15
Byers Ck 8/90	Rainbow trout	YES	13.03	-23.29
L Pass Ck 8/90	Rainbow trout	YES	10.48	-24.53
L Pass Ck 8/90	Rainbow trout	YES	13.34	-22.18
L Pass Ck 8/90	Rainbow trout	YES	10.02	-25.6
L Pass Ck 8/90	Rainbow trout	YES	14.37	-22.98
L Pass Ck 8/90	Rainbow trout	YES	13.82	-22.43
L Pass Ck 8/90	Rainbow trout	YES	13.9	-23.84
L Pass Ck 8/90	Rainbow trout	YES	14.67	-23.79
Clear Ck Clear 5/93	Coho alevin	YES	15.22	-22.48
Fish Ck Talkeetna 5/93	Coho alevin	YES	14.16	-22.44
EF Chulitna R 6/90	Coho alevin	YES	12.59	-27.17
Byers Ck 6/90	Coho alevin	YES	12.87	-22.32

L Pass Ck 6/90	Coho alevin	YES	13.39	-22.88
L Troublesome Ck 6/90	Coho alevin	YES	13.26	-22.73
Byers Ck 10/90	Coho fry	YES	10.73	-26.19
Byers Ck 8/90	Coho fry	YES	9.84	-27.37
Byers Ck 10/90	Coho fry	YES	9.05	-25.51
Clear Ck Clear 11/93	Coho fry	YES	5.46	-35.46
Clear Ck Clear 5/93	Coho fry	YES	10.05	-33.06
Clear Ck Clear 5/93	Coho fry	YES	9.15	-32.9
EF Chulitna R 8/90	Coho fry	YES	6.31	-28.53
EF Chulitna R10/90	Coho fry	YES	5.57	-29.37
Honolulu Ck 10/90	Coho fry	YES	5.9	-27.21
Honolulu Ck 10/90	Coho fry	YES	6.45	-28.32
Honolulu Ck 10/90	Coho fry	YES	7.1	-26.98
L Pass Ck 8/90	Coho fry	YES	7.9	-26.62
L Pass Ck 8/90	Coho fry	YES	8.27	-25.85
L Troublesome Ck 7/90	Coho fry	YES	9.09	-23.07
L Pass Ck 10/90	Coho fry	YES	10.99	-24.44
L Pass Ck 10/90	Coho fry	YES	10.98	-24.69
L Pass Ck 8/90	Coho fry	YES	6.18	-29.49
Fish Ck Talkeetna 6/93	Lamprey	YES	7.76	-34.5
Nancy Lk Ck 6/93	Lamprey	YES	7.01	-33.01
Nancy Lk Ck 6/93	Lamprey	YES	6.58	-31.31
Nancy Lk Ck 6/93	Lamprey	YES	6.07	-30.02
Byers Ck 8/93	Longnose Sucker	YES	9.69	-25.53
Byers Ck 8/93	Longnose Sucker	YES	11.66	-22.73